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TABLE OF CONTENTS

	PAGE
A Host Index to the North American Species of the Genus Cercospora...... ....Catharine Lieneman	1–52
Studies on the Growth of Root Hairs in Solutions. IX. The pH-Molar Rate Relation for Collards in Calcium Nitrate........................Clifford H. Farr	53–81
Hysterangium in North America........ ....S. M. Zeller and C. W. Dodge	83–128
Variation in Aster anomalus........Edgar Anderson	129–144
Some Chemical and Physiological Studies on the Nature and Transmission of "Infectious Chlorosis" in Variegated Plants ....Everett F. Davis	145–226
A Monograph of the Helicosporous Fungi Imperfecti......................David H. Linder	227–388
New Agaves from Southwestern United States..J. M. Greenman and Eva M. Fling Roush	389–392
Studies in the Umbelliferae. II...Mildred E. Mathias	393–398
Notes on Southwestern Plants...Mildred E. Mathias	399–404
A New Variety of Senecio aureus L...J. M. Greenman	405–406
Studies in the Apocynaceae. IIIA. A new Species of Amsonia from the South-Central States............Robert E. Woodson, Jr.	407–410
Preliminary Studies in the Genus Daldinia ....Marion Child	411–486
The Life History and Cytology of Saccoblastia intermedia, n. sp........David H. Linder	487–498
Non-Symbiotic Germination of Orchids ....Roland V. La Garde	499–514
General Index to Volume XVI....................	515–519

Annals of the Missouri Botanical Garden

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A HOST INDEX TO THE NORTH AMERICAN SPECIES OF THE GENUS CERCOSPORA

CATHARINE LIENEMAN

Instructor in the Henry Shaw School of Botany of Washington University

Introduction

The genus *Cercospora* belongs to the Fungi Imperfecti, Order Moniliales (Hyphomycetes), and Family Dematiaceae. To which section of the family the genus should be referred is a point on which some difference of opinion exists. Since the spores are many times longer than broad the logical position of the genus would seem to be in the section Scolecosporae. Lindau, in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien,' assigns it to this position as does Saccardo in his 'Sylloge Fungorum' **14**: 1099. 1899. However, in the earlier volumes of the 'Sylloge Fungorum' Saccardo included it in the Phragmosporae, and in this he was followed by Lindau in Rabenhorst's 'Kryptogamenflora.'

Since the published descriptions of the genus are very brief the following diagnosis is presented:

Fungi parasitic on herbaceous plant parts, especially leaves, more rarely on pedicels, stems, fruits, and bracts, usually forming definitely amphigenous necrotic spots which may become confluent and involve large areas of the leaf. Mycelium internal, filamentous, septate. Conidiophores usually emerging from the host tissue in fascicles, often by way of the stomata, usually easily visible with a hand lens, mostly hypophyllous, though frequently epiphyllous, smoky to brown in color, becoming darker with age but usually paler at the tip, simple or occasionally branched, cylindrical, wavy or geniculate with age, obtuse at the apex, usually septate when mature. Conidia borne singly and terminally on the conidiophore or becoming lateral by further

growth of the conidiophore tip, usually obclavate and attached by the broader base, often considerably attenuated at the apex, many times longer than broad, subhyaline to brown, or rarely entirely hyaline, smooth, at first aseptate, later becoming several- to many-septate, the usual range in length varying between 30 and 150 μ, with an average width of 3 to 6 μ, straight or curved.

The species of the genus *Cercospora* are usually typical leaf-spotting fungi. Under the hand-lens the conidiophores are usually visible as dark-colored tufts of projecting hyphae. In some cases they are too short to be individually recognizable under the lens and the tuft may appear as a very small projecting pustule. The color of the conidiophores and conidia is dark by reflected light, and this point usually enables one to distinguish this fungus from species of *Ramularia,* in which the spores and conidiophores are paler and appear whitish under the lens. Under the microscope, and especially in cross-sections of the leaf, these conidiophores are often seen to be confluent at their bases in a sub-stromatic or tubercular mass that, in many cases at least, is located in the sub-stomatal vesicle of the host plant. Emerging from the host, the conidiophores in the individual tufts may stand almost erect in the fascicle; in other cases they diverge at varying angles; and at times they become almost decumbent. When the conidiophores are erect they may be so closely bound together that the fascicle simulates a coremium such as present in *Isariopsis.*

The mode of formation of the conidia is such that while young conidiophores may be almost straight and smooth-walled, the older ones are likely to become wavy or irregular in outline. The first conidium is produced at the tip of a conidiophore. Then by further growth from a point near the place of attachment of this conidium the tip continues, usually at a slight angle to the direction of its previous growth, and then produces another conidium. This process may be repeated several times. Sometimes the direction of secondary growth is almost at right angles to that of the main axis of the conidiophore, in which case the tip of the conidiophore is sharply bent. The point of attachment of each conidium is usually visible after the conidium has fallen, so that the number of conidia that any conidiophore has pro-

duced can be rather easily determined. It follows then that the older conidiophores may present quite a different appearance from those that are producing their first crop of conidia. This is also correlated with a deepening in color, so that the older conidiophores are both more irregular and darker than are the younger ones. This point should be borne in mind in determining specific limitations.

As in the case of all fungi with septate and elongated spores, the growth of the conidium and the formation of the septae is a continuous process, so that young spores may be much shorter and lack septae or have a lesser number of septae than do mature spores of the same species. Because of this fact, undoubtedly many species that have been recognized as distinct from others on the basis of smaller conidia with fewer septae are in reality only immature forms of other species.

History

The early use of the name *Cercospora* is difficult to follow, notwithstanding the fact that it was not proposed until 1863. In that year Fuckel issued his exsiccati entitled 'Fungi Rhenani,' of which numbers 117 to 120 are species of *Cercospora* and are so designated. The characterization "Cercospora Fres. Passalora valde affinis est, sed constanter sporidiis multiseptatis differt." (No. 117) probably satisfies the requirements of generic diagnosis according to the International Code. In the same year (1863) Fresenius published his 'Beiträge zur Mykologie,' in which (pp. 91–93) he fails to give a formal description of *Cercospora* but refers to it and describes *C. Apii*, *C. Chenopodii*, *C. penicillata*, and *C. ferruginea*, some of which he had apparently received from Fuckel, to whom he attributes the last-named species. Fresenius remarks that the specimens sent by Fuckel could not be classified with previously described genera because of the elongated conidia (p. 92, under *C. Apii*). The characters on which he recognized these species as constituting a generic entity are not succinctly stated, yet enough is given for the recognition of the group. It would appear that Fuckel's 'Fungi Rhenani' was issued almost simultaneously with Fresenius' 'Beiträge zur Mykologie' but it is probably not possible

to decide which actually appeared first. Under the circumstances *C. Apii* Fres. would seem to be the type species of the genus.

Fresenius delimits the genus *Cercospora* on the following characters which we find mentioned in the notes and in the description of the type species, *C. Apii:* brown conidiophores borne in fascicles, simple, erect or nearly so, bearing hyaline bristle-like spores. The conidiophores are non-septate or sometimes show a cross-wall above the base. At their apices and along the sides there are dark scars from fallen conidia. The spores are bristle-like with clavate thickened bases and gradually attenuated apices; they are erect or bent in various ways at the apex. The septations in the conidia vary from three to eleven.

All of the members of the genus *Cercospora* described in Fresenius' 'Beiträge zur Mykologie' agree in having brown conidiophores but the color of the conidia themselves as there described varies from hyaline (*C. Apii*) to brown (*C. ferruginea*). The shape of both spores and conidiophores varies little. If the spores of *C. Apii*[1] are in reality hyaline, and that species be taken as the type of the genus, then it becomes impossible to limit the genus *Cercospora* to brown-spored species.

Saccardo, in Michelia **2**: 20. 1880, described the genus *Cercosporella* which may be regarded, in part at least, as a segregate from *Cercospora*. The first two species mentioned by him are *Cercosporella persica* Sacc. and *C. cana* Sacc., both of which had been previously described by him under the genus *Cercospora*. The separation into the new genus *Cercosporella* was made on the basis of the presence in these species of hyaline conidiophores and conidia. This genus has been commonly accepted, and to it have been transferred a considerable number of hyaline-spored species of *Cercospora*. However, a great deal of work yet remains to be done before the exact status of many species now under *Cercospora* can be determined.

As stated above, the genus *Cercospora* as originally proposed by Fresenius, in 1863, contained four species there described for the first time. Fuckel in his 'Symbolae Mycologici,' 1869–70,

[1] The spores vary from hyaline to brown according to reports. Stevens describes them as hyaline; Schwarze hyaline to brown.

enumerated 10 species. Saccardo, in Michelia, 1877–1882, described approximately 60 species. Cooke in Grevillea, 1876–1885, has described some 37 additional species. Since then, Ellis and his co-workers have described more than 150 American species. This number has been augmented by various workers, such as Peck who has described at least 30 species, Atkinson with 40 or more, Kellerman and Swingle with 7 or 8, Tehon and Daniels with approximately a dozen, Tharp with 30 or more, and Heald and Wolf with 20 or more.

Nomenclature and Citations

In working out the nomenclature of the host species an attempt has been made to follow the International Code as exemplified in Gray's 'New Manual of Botany,' 7th edition, and Bailey's 'Manual of Cultivated Plants,' except in such cases where it has seemed more expedient to follow volumes 1 and 2 of the 'Index Kewensis.' For the nomenclature of the species of the genus *Cercospora* the International Code has been used throughout.

In several cases quotations concerning the relationships of the species have been introduced. Unless these are specifically attributed to a particular author, they are always the comments of the original author of the species.

It has been thought worth while to give with each species such additional references as might be of service in confirming an identification reached by means of the host index. Therefore in citing the literature of *Cercospora* the first citation is to the original place of publication of the binomial in question. If another citation intervenes between this and the citation in 'Sylloge Fungorum,' provided that the *Cercospora* was described previous to the appearance of volume 22, it constitutes the original description of the fungus under another name. The 'Sylloge Fungorum' reference appears next, followed by whatever other descriptions may have been found in looking over available literature. For most species the next most important reference is Ellis and Everhart's 'Enumeration of the North American Cercosporae' which began in the first number of the Journal of Mycology (1885) and was continued through volume 4 (1888). The work was not intended as a monograph, but simply a compila-

tion of species known at that time. Because they contain descriptions of a considerable number of species, the articles by Atkinson (Jour. Elisha Mitchell Sci. Soc. 8: 33–67. 1892) and by Schwarze (N. J. Agr. Sta. Bull. 313. 1917) are consistently cited for the species they contain. Wherever the United States Department of Agriculture Bulletin 1366 or the 'Scientific Survey of Porto Rico' is mentioned, it should be borne in mind that these are merely lists of hosts and their attacking fungi and contain no descriptive matter. Similarly, the Transactions of the Wisconsin Academy of Sciences, Arts, and Letters is frequently cited, when no description is given, because a new host is listed or the geographical range is extended.

The Scope and Arrangement of the Index

Only those plants indigenous to the continent of North America which are hosts to *Cercospora* are cited. An attempt has been made to list the International Code name; synonyms appear in italics and their equivalents follow in ordinary type. In the "Host Index" the hosts included in a bracket are affected by the same species of *Cercospora*. In the "Index of Species of Cercospora" where literature citations are given, each species is preceded by a number. This number appears again as a cross-reference in "Host Families and their Cercosporas" where the Cercosporas are arranged according to the host families they affect.

Acknowledgments

The writer wishes especially to thank Dr. L. O. Overholts, of Pennsylvania State College, formerly Mycologist to the Missouri Botanical Garden, for his unremitting enthusiasm and help in the preparation of this paper. Thanks are also due Dr. George T. Moore, Director of the Garden, for the facilities of the herbarium and library; to Mr. T. J. Fitzpatrick, Librarian, University of Nebraska, for the use of his personal library and that of the university; to Dr. J. M. Greenman and Miss Mildred Mathias, of the Missouri Botanical Garden, and to Dr. John Hendley Barnhart, Bibliographer, New York Botanical Garden, for help in nomenclatorial problems; to Miss Nell Horner, for checking and reading proof of this paper; and to all others who so kindly helped in the preparation of this paper.

Abbreviations of Authors

Herewith is appended a list of the abbreviations for the names of authors, and for titles of publications cited:

Allesch. = Allescher, A.
Atk. = Atkinson, G. F.
Barth. = Bartholomew, E. T.
Berk. = Berkeley, M. J.
Berl. = Berlese, A. M.
Br. = Broome, C. E.
Bres. = Bresadola, G.
Casp. = Caspary, R.
Ces. = Cesati, V.
Clint. = Clinton, G. P.
Curt. = Curtis, M. A.
Dearn. = Dearness, J.
Desm. = Desmazieres, J.
Ell. = Ellis, J. B.
Ev. = Everhart, B. M.
Fckl. = Fuckel, L.
Fres. = Fresenius, G.
Gall. = Galloway, B. T.
Ger. = Gerard, W. R.
Halst. = Halsted, B. D.
Harkn. = Harkness, H. W.
Henn. = Hennings, P.
Holw. = Holway, E.
Kell. = Kellermar, W.
Langl. = Langlois, L. B.
Lév. = Léveillé, J. H.
Mart. = Martin, G.
Massal. = Massalongo, C.
Oud. = Oudemans, C. A.
Pass. = Passerini, G.
Pat. = Patouillard, N.
Penz. = Penzig, O.
Rab. = Rabenhorst, L.
Racib. = Raciborski, M.
Rav. = Ravenel, H. W.
Roum. = Roumeguere, C.
Sacc. = Saccardo, P. A.
Sacc.D. = Saccardo, D.
Schn. = ? Schneider, W. G.
Sorok. = Sorokin, N.
Speg. = Spegazzini, C.
Sw. = Swingle, W.
Sydow = Sydow, H. & P.
Thuem. = de Thuemen, F.
Westd. = Westendorp, G. D.
Wint. = Winter, G.

Abbreviations of Publications

Acad. Phila. Proc. = Proceedings of the Academy of Natural Sciences of Philadelphia.
Acad. Roy. Sci. Belgique Bull. = Bulletins de l'Academie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique.
Ala. Agr. Sta. Bull. = Alabama Agricultural Experiment Station Bulletin.
Am. Nat. = The American Naturalist.
Ann. Mag. Nat. Hist. = Annals and Magazine of Natural History.
Ann. Myc. = Annales Mycologici.
Ann. Sci. Nat. Bot. = Annales des Sciences Naturelles. Botanique.
B. P. I. Bull. = United States Department of Agriculture—Bureau of Plant Industry Bulletin.
Beitr. Myk. = Beiträge zur Mykologie.
Bot. Gaz. = Botanical Gazette.
Bot. Univ. Pavia Atti = Atti dell' Istituto Botanico dell' Universita di Pavia.
Calif. Acad. Sci. Bull. = California Academy of Sciences Bulletin.
Can. Inst. Proc. = Proceedings of the Canadian Institute.
Can. Inst. Trans. = Transactions of the Canadian Institute.

Can. Rec. Sci.	= Canadian Record of Science.
Cornell Univ. Bull.	= Bulletin of Cornell University.
Dec. Myc.	= Decades Mycologicae Italicae.
Elisha Mitchell Sci. Soc. Jour.	= Journal of the Elisha Mitchell Scientific Society.
Field Mus. Bot. Ser. Rept.	= Field Columbian Museum Report—Botanical Series.
Fla. Agr. Sta. Bull.	= Florida Agricultural Experiment Station Bulletin.
Fungi Columb.	= Fungi Columbiana.
Grev.	= Grevillea.
Guar.	= Fungi Guarantici.
Harriman Alaska Exped.	= Harriman Alaska Expedition.
Hedw.	= Hedwigia.
Ill. Acad. Trans.	= Transactions of the Illinois Academy of Science.
Ind. Acad. Proc.	= Proceedings of the Indiana Academy of Science.
Iowa Acad. Proc.	= Proceedings of the Iowa Academy of Science.
Ist. Veneto Atti	= Atti R. Istituto Veneto di Scienze, Lettere ed Arti.
Jour. Myc.	= Journal of Mycology.
K. Akad. Wiss. Berlin Monatsber.	= Monatsberichte der Königlichen Akademie der Wissenschaft Berlin.
Linn. Soc. Bot. Jour.	= Journal of Linnaean Society—Botany. London.
Mededeel. Proefst. Suiker.	= Mededeelingen van het Proefstation voor de Java Suikerindustrie.
Mich. Agr. Sta. Tech. Bull.	= Michigan Agricultural Experiment Station Technical Bulletin.
Misc. myc.	= Miscellanea mycologica.
Mo. Bot. Gard. Ann.	= Annals of the Missouri Botanical Garden.
Myc.	= Mycologia.
Myc. Univ.	= Mycotheca Universalis.
Myc. Ven.	= Mycotheca Veneta.
Not. Myc.	= Notae Mycologicae.
N. J. Agr. Sta. Bull.	= New Jersey Agricultural Experiment Station Bulletin.
Nuovo Giorn. Bot. Ital.	= Nuovo Giornale Botanico Italiano.
N. Y. Acad. Ann.	= Annals of the New York Academy of Sciences.
N. Y. Bot. Gard. Bull.	= New York Botanical Garden Bulletin.
N. Y. Mus. Rept.	= State Museum Report—University of the State of New York.
Oest. Bot. Zeitschr.	= Oesterreichische botanische Zeitschrift.
Phytopath.	= Phytopathology.
Rev. Myc.	= Revue Mycologique.
Sci. Surv. Porto Rico	= Scientific Survey of Porto Rico and the Virgin Islands.
Soc. Cien. Argent. Ann.	= Annales de la Sociedad Cientifiques Argentina.

Soc. Myc. Fr. Bull.	= Bulletin de la Société Mycologique de France.
Syll. Fung.	= Sylloge Fungorum.
Symb. Myc.	= Symbolae Mycologicae.
Tex. Agr. Sta. Bull.	= Texas Agricultural Experiment Station Bulletin.
Tokyo Coll. Agr. Jour.	= Journal of the College of Agriculture, Imperial University of Tokyo.
Torr. Bot. Club Bull.	= Bulletin of the Torrey Botanical Club.
Tuskegee Sta. Bull.	= Tuskegee Experiment Station Bulletin.
Wisc. Acad. Trans.	= Transactions of the Wisconsin Academy of Sciences, Arts, and Letters.
Univ. Maine Studies	= University of Maine Studies.
U. S. D. A. Bull.	= United States Department of Agriculture Bulletin.
Zeit. Pflanzenkr.	= Zeitschrift für Pflanzenkrankheiten.

Host Index

Abelmoschus esculentus (L.) Moench = Hibiscus esculentus L.
Abutilon Avicennae Gaertn. = A. Theophrasti Medic.
Abutilon Theophrasti Medic.
  C. Abutilonis Tehon & Daniels
  C. Althaeina Sacc.
Acalypha caroliniana Ell. = A. ostryaefolia Ridd.
Acalypha graciliens Gray
  C. Acalyphae Peck
Acalypha ostryaefolia Ridd.
  C. Acalyphae Peck
  C. Acalypharum Tharp
Acalypha virginica L.
  C. Acalyphae Peck
Acer Negundo L.
  C. Negundinis Ell. & Ev.
Acerates viridiflora (Raf.) Eaton
  C. Briareus Ell. & Ev.
Achyranthes portoricensis (Kuntze) Standl.
  C. Alternantherae Ell. & Langl.
Acnida cannabina L.
  C. Acnidae Ell. & Ev.
Actinomeris alternifolia (L.) DC.
  C. anomala Ell. & Halst.
Actinomeris squarrosa Nutt. = A. alternifolia (L.) DC.
Acuan illinoense (Michx.) Kuntze = Desmanthus illinoensis (Michx.) Mac M.
Aesculus octandra Marsh
  C. Aesculina Ell. & Kell.
Agrostis sp.
  C. Agrostidis Atk.
Ailanthus glandulosa Desf.
  C. glandulosa Ell. & Kell.
Alisma Plantago-aquatica L. ex Am. Auth.
  C. Alismatis Ell. & Holw.
  C. pachyspora Ell. & Ev.
Alisma subcordatum Raf. = A. Plantago-aquatica L.
Allionia hirsuta Pursh = Oxybaphus hirsutus (Pursh) Sweet
Allionia nyctaginea Michx. = Oxybaphus nyctagineus (Michx.) Sweet
{Alternanthera Achyrantha R. Br.,
Alternanthera portoricensis (Kuntze) Standl.
  C. Alternantherae Ell. & Langl.
Althaea rosea Cav.
  C. Althaeina Sacc.
  C. Kellermani Bubák
Amaranthus sp.
  C. brachiata Ell. & Ev.
  C. canescens Ell. & Mart.
{Amaranthus retroflexus L.
Amaranthus spinosus L.
  C. brachiata Ell. & Ev.
Amaryllis sp.
  C. Amaryllidis Ell. & Ev.

Ambrosia trifida L.
C. Arcti-Ambrosiae Halst.
C. racemosa Ell. & Mart.
Amelanchier sp.
C. Mali Ell. & Ev.
Ammania coccinea Rottb.
C. Ammanniae Tharp
Ammania latifolia Torr. & Gray, not L. = A. coccinea Rottb.
Amorpha canescens Pursh
C. Passaloroides Wint.
Amorpha cordata
C. Vitis (Lév.) Sacc.
Amorpha fruticosa L.
C. Passaloroides Wint.
Ampelopsis sp.
C. Ampelopsidis Peck
Ampelopsis arborea (L.) Rusby = Cissus arborea (L.) DesMoulins
Ampelopsis cordata Michx. = Cissus Ampelopsis Pers.
Ampelopsis quinquefolia (L.) Michx. = Psedera quinquefolia (L.) Greene
Amphicarpaea comosa Nwd. & Lunell
C. simulans Ell. & Kell.
Amphicarpa monoica (L.) Ell.
C. monoica Ell. & Holw.
C. simulans Ell. & Kell.
Amygdalus spp. = Prunus spp.
Andropogon halepensis (L.) Brot. = Holcus halepensis L.
Anethum graveolens L.
C. Anethi Sacc.
Angelica ?
C. Apii Fres. var. *Angelicae* Sacc. & Scalia
Angelica hirsuta Muhl. = A. villosa (Walt.) BSP.
Angelica villosa (Walt.) BSP.
C. Thaspii Ell. & Ev.
Apios tuberosa Moench
C. tuberosa Ell. & Kell.
Apium graveolens L.
C. Apii Fres.
Apocynum sp.
C. Apocyni Ell. & Kell.
Aquilegia canadensis L.
C. Aquilegiae Kell. & Sw.
Arachis hypogaea L.
C. personata (Berk. & Curt.) Ell.
Aralia nudicaulis L.
C. leptosperma Peck
Aralia spinosa L.
C. atromaculans Ell. & Ev.
Archangelica hirsuta Torr. & Gray = Angelica villosa (Walt.) BSP.
Arctium Lappa L.
C. Arcti-Ambrosiae Halst.
Arctostaphylos Uva-ursi (L.) Spreng.
C. Arctostaphyli Davis
Argythamnia mercurialina Muell.
C. Argythamniae Dearn. & House
Aristolochia macrophylla Lam.
C. guttulata Ell. & Kell.
Aristolochia Serpentaria L.
C. Serpentariae Ell. & Ev.
Armoracia rusticana Gaertn. Mey. & Scherb.
C. Armoraciae Sacc.
Aronia arbutifolia (L.) Ell. = Pyrus arbutifolia (L.) L. f.
{Artemisia Absinthium L.
{Artemisia ludoviciana Nutt.
C. Absinthii (Peck) Sacc.
Artemisia vulgaris L.
C. ferruginea Fckl.
Arundinaria tecta (Walt.) Muhl.
C. Scolecotrichoides Atk.
Asclepias amplexicaulis J. E. Smith
C. clavata (Ger.) Peck
Asclepias cordifolia (Benth.) Jep. = Gomphocarpus cordifolius Benth.
Asclepias Cornuti Decne. = A. syriaca L.
Asclepias curassavica L.
C. venturioides Peck
Asclepias ecornuta Kell. = Gomphocarpus cordifolius Benth.
Asclepias incarnata L.
C. clavata (Ger.) Peck
C. incarnata Ell. & Ev.
Asclepias Jamesii Torr. & Gray = A. latifolia (Torr.) Raf.
Asclepias latifolia (Torr.) Raf.
C. Asclepiodorae Ell. & Kell.
Asclepias Meadii Torr.
C. clavata (Ger.) Peck

Asclepias obtusifolia Michx. = A. amplexicaulis J. E. Smith

Asclepias phytolaccoides Pursh
Asclepias speciosa Torr.
C. *clavata* (Ger.) Peck

Asclepias syriaca L.
C. *clavata* (Ger.) Peck
C. *elaeochroma* Sacc.
C. *Hanseni* Ell. & Ev.
C. *illinoensis* Barth.
C. *venturioides* Peck

Asclepias tuberosa L.
Asclepiodora sessilis
Asclepiodora viridis (Walt.) Gray
C. *Asclepiodorae* Ell. & Kell.

Asimina triloba Dunal
C. *Asiminae* Ell. & Kell.

Asparagus officinalis L.
C. *Asparagi* Sacc.
C. *caulicola* Wint.

Aster sp.
C. *Asterata* Atk.
C. *viminei* Tehon

Aster vimineus Lam.
C. *viminei* Tehon

Atriplex patula L.
C. *dubia* (Riess) Wint.

Baccharis Douglasii DC.
C. *Baccharidis* Ell. & Ev.

Baptisia sp.
Baptisia bracteata (Muhl.) Ell.
Baptisia leucantha Torr. & Gray
C. *velutina* Ell. & Kell.

Begonia sp.
C. sp.—reported in Tex. Agr. Sta. Bull. **9**: 24. 1890, Jour. Myc. **6**: 83. 1891, and in U. S. D. A. Bull. 1366. 1926, without description.

Beta vulgaris L.
C. *beticola* Sacc.

Bidens sp.
C. *umbrata* Ell. & Holw.

Bidens cernua L.
Bidens connata Muhl.
C. *megalopotamica* Speg.

Bidens Nashii Small
C. *Bidentis* Tharp

Bignonia capreolata L.
C. *capreolata* Ell. & Ev.

Bignonia crucigera L., in part = B. capreolata L.

Bignonia radicans L. = Campsis radicans (L.) Seem.

Blitum capitatum L. = Chenopodium capitatum (L.) Asch.

Boehmeria cylindrica (L.) Sw.
C. *Boehmeriae* Peck

Borreria micrantha Torr. & Gray
C. *Borreriae* Ell. & Ev.

Brassica oleracea capitata L.
C. *Bloxami* Berk. & Br.

Breweria humistrata (Walt.) Gray
C. *Stylismae* Tracy & Earle

Brickellia californica (Kuntze) Gray
C. *Coleosanthi* Ell. & Ev.

Buchloë dactyloides (Nutt.) Engelm.
C. *seminalis* Ell. & Ev.

Bumelia lanuginosa (Michx.) Pers.
C. *lanuginosa* Heald & Wolf

Calla palustris L.
C. *Callae* Peck & Clint.

Callicarpa sp.
Callicarpa americana L.
C. *Callicarpae* Cooke

Callirhoë sp.
Callirhoë involucrata (Torr. & Gray) Gray
C. *Althaeina* Sacc.

Callirhoë triangulata (Leavenw.) Gray
C. *Althaeina* Sacc. var. *praecincta* Davis

Campsis radicans (L.) Seem.
C. *duplicata* Ell. & Ev.
C. *Langloisii* Sacc.
C. *sordida* Sacc.

Camptosorus rhizophyllus (L.) Link
C. *Camptosori* Davis

Capsicum annuum L. = C. frutescens L.

Capsicum frutescens L.
C. *Capsici* Heald & Wolf

Carduus altissimus L. = Cirsium altissimum (L.) Spreng.

Carex arctata Boott
Carex castanea Wahlenb.
Carex cephaloidea Dewey
C. *Caricina* Ell. & Dearn.

Carex folliculata L.
C. *Caricis* Dearn. & House

Carex gracillima Schwein.
Carex grisea Wahlenb.
Carex intumescens Rudge
  C. Caricina Ell. & Dearn.
Carex laxiflora Lam.
  C. microstigma Sacc.
Carex lupulina Muhl.
Carex retrorsa Schwein.
Carex rosea Schkuhr.
  C. Caricina Ell. & Dearn.
Carum Petroselinum Benth. & Hook. = Petroselinum hortense Hoff.
Carya alba (L.) K. Koch
  C. Halstedii Ell. & Ev.
Carya illinoensis (Wang.) K. Koch
  C. fusca (Heald & Wolf) emend. F. V. Rand, acc. to U. S. D. A. Bull. 1366. 1926.
Carya olivaeformis Nutt. = C. illinoensis (Wang.) K. Koch
Carya tomentosa Nutt. = C. alba (L.) K. Koch
Casimiroa edulis La Llave
  C. Coleroides Sacc.
Cassava sp.
  C. Cassavae Ell. & Ev.
Cassia alata L.
  C. Chamaecristae Ell. & Kell.
  C. simulata Ell. & Ev.
Cassia Chamaecrista L.
  C. Chamaecristae Ell. & Kell.
Cassia marilandica L.
  C. simulata Ell. & Ev.
Cassia nictitans L.
  C. pinnulaecola Atk.
Cassia obtusifolia L. = C. Tora L.
Cassia occidentalis L.
  C. Chamaecristae Ell. & Kell.
  C. occidentalis Cooke
  C. personata (Berk. & Curt.) Ell. & Ev. var. *Cassiae occidentalis* Sacc.
Cassia Tora L.
  C. atromaculans Ell. & Ev.
  C. nigricans Cooke
  C. Torae Tharp
Castalia odorata (Ait.) Woodville & Wood
Castalia tuberosa (Paine) Greene
  C. Nymphaeacea Cooke & Ell.
Castilleja pallida Kunth
  C. sp. acc. to Iowa Acad. Proc. **27:** 105. 1920.
Catalpa bignonioides Walt.
  C. Catalpae Wint.
Catalpa Catalpa Karst. = C. bignonioides Walt.
Catalpa speciosa Warder
  C. Catalpae Wint.
Cathartolinum virginianum (L.) Reichenb. = Linum virginianum L.
Caulophyllum thalictroides (L.) Michx.
  C. Caulophylli Peck
Ceanothus americanus L.
  C. Ceanothi Kell. & Sw.
Ceanothus arboreus Greene
  C. MacClatchieana Sacc. & Syd.
Ceanothus ovatus Desf.
  C. Ceanothi Kell. & Sw.
Cebatha carolina (L.) Britt. = Coccolus carolinus (L.) DC.
Celastrus scandens L.
  C. melanochaeta Ell. & Ev.
Cephalanthus occidentalis L.
  C. Cephalanthi Ell. & Kell.
  C. perniciosa Heald & Wolf
Cercis canadensis L.
  C. cercidicola Ell.
  C. cercidicola Ell. var. *coremioides* Tehon
Cercis occidentalis Torr.
  C. cercidicola Ell.
Chaetochloa glauca (L.) Scribn. = Setaria glauca (L.) Beauv.
Chamaecrista nictitans (L.) Moench = Cassia nictitans L.
Chayota edulis Jacq. = Sechium edule (Jacq.) Sw.
Chenopodium album L.
  C. dubia (Riess) Wint.
Chenopodium ambrosioides L. var. anthelminthicum (L.) Gray
  C. anthelmintica Atk.
Chenopodium capitatum (L.) Asch.
  C. dubia (Riess) Wint.
Chionanthus virginica L.
  C. Chionanthi Ell. & Ev.
Chloris petraea Sw.
Chloris Swartziana Doell.
  C. caespitosa Ell. & Ev.

Chrysanthemum sp.
C. Chrysanthemi Heald & Wolf
Chrysobalanus oblongifolius Michx.
C. Chrysobalani Ell. & Ev.
Chrysopsis graminifolia (Michx.) Nutt.
C. macroguttata Atk.
Cichorium Intybus L.
C. Cichorii Davis
Cinchona sp.
C. Cinchonae Ell. & Ev.
Cirsium sp.
C. kansensis Syd.
C. obesa Ell. & Ev.
Cirsium altissimum (L.) Spreng.
C. kansensis Syd.
Cirsium remotifolium (Gray) Jeps.
C. Cirsii Ell. & Ev.
Cirsium undulatum (Nutt.) Spreng.
C. ditissima Ell. & Ev.
Cissus Ampelopsis Pers.
C. truncata Ell. & Ev.
Cissus arborea (L.) DesMoulins
C. arboriae Tharp
Citrullus Citrullus (L.) Small = C. vulgaris Schrad.
Citrullus vulgaris Schrad.
C. Citrullina Cooke
Citrus Aurantium L.
C. aurantia Heald & Wolf
Citrus sinensis Pers. = C. Aurantium L.
Clematis sp.
C. rubigo Cooke & Harkn.
{Clematis viorna L.
{Clematis virginiana L.
C. squalidula Peck
Cleome sp.
C. conspicua Earle
Cleome pungens Willd. = C. spinosa L.
Cleome spinosa L.
C. Cleomis Ell. & Halst.
C. conspicua Earle
{Clitoria mariana L.
{Clitoria virginiana L.
C. Clitoriae Atk.
Cnicus sp. = Cirsium sp.
Cnicus remotifolius Gray = Cirsium remotifolium (Gray) Jeps.
Cnicus undulatus (Nutt.) Gray = Cirsium undulatum (Nutt.) Spreng.
Coccolus carolinus (L.) DC.
C. Menispermi Ell. & Holw.
Coffea arabica L.
C. coffeicola Berk. & Curt.
C. Herrerana Farneti
Coleosanthus californicus Kuntze = Brickellia californica (Kuntze) Gray
Comandra umbellata (L.) Nutt.
C. Comandrae Ell. & Dearn.
Comarum palustre L. = Potentilla palustris (L.) Scop.
Convolvulus acetosaefolius R. & S. = Ipomoea stolonifera (Cyrill.) Poir.
Convolvulus sepium L.
C. tuberculella Davis
Cornus femina Mill.
C. Corni Davis
Cornus florida L.
C. cornicola Tracy & Earle
Cornus paniculata L'Her.
C. Corni Davis
Cracca hispidula (Michx.) Kuntze = Tephrosia hispidula (Michx.) Pers.
Crassina elegans (Jacq.) Kuntze = Zinnia elegans Jacq.
Crataegus sp.
C. confluens Lieneman, nom. nov.
Crataegus apiifolia Michx. = C. Marshallii Eggl.
Crataegus Marshallii Eggl.
C. Apiifoliae Tharp
Crinum sp.
C. Pancratii Ell. & Ev.
Crotalaria sagittalis L.
C. Demetrioniana Wint.
Croton sp.
C. Crotonis Ell. & Ev.
Croton capitatus Michx.
C. capitati Tharp
Croton fruticulosus Engelm.
C. crotonicola Ell. & Barth.
Croton glandulosus L.
C. crotonifolia Cooke
Croton maritimus Walt.
C. maritima Tracy & Earle
Croton texensis (Klotzsch) Muell. Arg.
C. Crotonis Ell. & Ev.
Cubelium concolor (Forst.) Raf. = Hybanthus concolor (Forst.) Spreng.

Cucumis sativus L.
C. sp.—cited in U. S. D. A. Bull. 1366. 1926.

Cucurbita sp.
C. cucurbitacea Ell. & Gall., acc. to U. S. D. A. Bull. 1366. 1926.

Cucurbita foetidissima HBK.
Cucurbita Lagenaria L.
Cucurbita maxima Duchesne
Cucurbita moschata Duchesne
Cucurbita Pepo L.
C. Cucurbitae Ell. & Ev.

Cucurbita perennis Gray = C. foetidissima HBK.

Cydonia japonica Pers. = Pyrus japonica (Pers.) Thunb.

Cynara Cardunculus L.
Cynara Scolymus L.
C. obscura Heald & Wolf

Cynoctonum Mitreola (L.) Britt.
C. torta Tracy & Earle

Cynoctonum petiolatum (Walt.) Gmel. = C. Mitreola (L.) Britt.

Cynoxylon floridum (L.) Raf. = Cornus florida L.

Cyperus filiculmis Vahl
Cyperus Houghtonii Torr.
Cyperus Schweinitzii Torr.
C. Caricina Ell. & Dearn.

Cypripedium acaule Ait.
Cypripedium hirsutum Mill.
Cypripedium parviflorum Salisb. var. pubescens (Willd.) Knight
C. Cypripedii Ell. & Dearn.

Cypripedium spectabile Salisb. = C. hirsutum Mill.

Dactyloctenium aegyptium (L.) Richter
C. tessellata Atk.

Dalea enneandra Nutt.
C. Daleae Ell. & Kell.

Dalea laxiflora Pursh = D. enneandra Nutt.

Dasystephana linearis (Froel.) Britt. = Gentiana linearis Froel.

Dasystoma virginica (L.) Britt. = Gerardia virginica (L.) BSP.

Datura Metel L.
C. crassa Sacc.

Datura Stramonium L.
C. crassa Sacc.
C. Daturae Peck

Daucus Carota L.
C. sp.—mentioned in U. S. D. A. Bull. 1366. 1926.

Decodon verticillatus (L.) Ell.
C. Decodontis Tehon & Daniels
C. Nesaeae Ell. & Ev.

Decumaria barbara L.
C. Decumariae Tracy & Earle

Desmanthus illinoensis (Michx.) MacM.
C. Desmanthi Ell. & Kell.

Desmodium acuminatum DC. = D. grandiflorum (Walt.) DC.

Desmodium grandiflorum (Walt.) DC.
Desmodium molle DC.
Desmodium nudiflorum (L.) DC.
C. Desmodii Ell. & Kell.

Desmodium tortuosum DC.
C. melaleuca Ell. & Ev.

Deutzia gracilis Sieb. & Zucc.
C. Deutziae Ell. & Ev.

Dianthera americana L.
C. Diantherae Ell. & Kell.

Diervilla sp.
C. Weigeliae Ell. & Ev.

Diervilla Lonicera Mill.
C. Diervillae Ell. & Ev.

Diervilla trifida Moench = D. Lonicera Mill.

Diodia teres Walt.
C. Diodiae Cooke

Diodia virginiana L.
C. Diodiae-virginianae Atk.

Dioscorea villosa L.
C. Dioscoreae Ell. & Mart.
C. nubilosa Ell. & Ev.

Diospyros Kaki L.
C. Diospyri Thuem.
C. fuliginosa Ell. & Kell.
C. Kaki Ell. & Ev.

Diospyros virginiana L.
C. atra Ell. & Ev.
C. Diospyri Thuem.
C. Diospyri Thuem. var. *ferruginosa* Atk.
C. flexuosa Tracy & Earle

C. *fuliginosa* Ell. & Kell.
C. *virginiana* Thuem.—cited in U. S. D. A. Bull. 1366. 1926.
Dipsacus sylvestris Huds.
C. *elongata* Peck
Dipteracanthus ciliosus Nees. = Ruellia parviflora (Nees) Britt.
Ditremexa occidentalis (L.) Britt. & Rose = Cassia occidentalis L.
Dolichos sp.
C. *cruenta* Sacc.
Dolichos Lablab L.
C. *canescens* Ell. & Mart.
Dolichos sinensis L. = Vigna sinensis (L.) Endl.
Echinochloa crusgalli (L.) Beauv.
C. *Echinochloae* Davis
Echinocystis lobata (Michx.) Torr. & Gray
C. *Echinocystis* Ell. & Mart.
Eichhornia speciosa Kunth
C. *Piaropi* Tharp
{Elaeagnus sp.
{Elaeagnus angustifolia L.
C. *Elaeagni* Heald & Wolf
Elephantopus carolinianus Willd.
C. *Elephantopodis* Ell. & Ev.
{Elephantopus caroliniensis G. F. W. Mey.[1]
{Elephantopus nudatus Gray
{Elephantopus tomentosus L.
C. *Elephantopodis* Ell. & Ev.
Eleusine aegyptia Pers. = Dactyloctenium aegyptium (L.) Richter
Epigaea repens L.
C. *Epigaeae* Ell. & Dearn.
C. *Epigaeina* Davis
Epilobium adenocaulon Haussk.
C. *montana* (Speg.) Sacc.
Epilobium alpinum L.
C. *Epilobii* Schn.
{Epilobium angustifolium L.
{Epilobium coloratum Muhl.
C. *montana* (Speg.) Sacc.
Erechthites hieracifolia (L.) Raf.
C. *Erechthitis* Atk.
Erechthites praealta Raf. = E. hieracifolia (L.) Raf.
Erigeron annuus (L.) Pers.
C. *grisella* Peck
Erigeron tomentosus[2]
C. *ferruginea* Fckl.
Eriogonum molle Greene
C. *Eriogoni* Ell. & Ev.
Eriogonum tomentosum Michx.
C. *rubella* Cooke
Erysimum cheiranthoides L.
C. *Erysimi* Davis
Erysimum officinale (L.) Scop. = Sisymbrium officinale Scop.
Erythrina Crista-galli L.
C. *Erythrinae* Ell. & Ev.
Erythrina herbacea L.
C. *erythrinicola* Tharp
{Euonymus americana L.
{Euonymus atropurpurea Jacq.
{Euonymus europaea L.
C. *Euonymi* Ell.
Euonymus japonica L.
C. *destructiva* Rav.
Eupatorium ageratoides L. = E. urticaefolium Reichard
Eupatorium album L.
C. *Ageratoides* Ell. & Ev.
C. *Eupatorii* Peck
{Eupatorium perfoliatum L.
{Eupatorium purpureum L.
C. *perfoliata* Ell. & Ev.
Eupatorium rotundifolium L.
C. *Eupatorii* Peck
Eupatorium urticaefolium Reichard
C. *Ageratoides* Ell. & Ev.
Eupatorium verbenaefolium Michx.
C. *Agrostidis* Atk.

[1] Although *C. Elephantopodis* was described in the original as occurring on *Elephantopus carolinensis*, a tropical species, the host is more likely to have been *Elephantopus carolinianus* Willd.

[2] Search through the available literature has failed to disclose this species of *Erigeron* as cited by Ellis and Everhart. Perhaps *Erigeron tomentosus* was an error for *Eriogonum tomentosum* Michx.

Euphorbia sp.
C. euphorbiaecola Atk.
Euphorbia corollata L.
C. Euphorbiae Kell. & Sw.
C. heterospora Ell. & Ev.
Euphorbia pulcherrima Willd.
C. pulcherrimae Tharp
C. pulcherrimae minima Tharp
Eustachys petraea (Sw.) Desv. = Chloris petraea Sw.
{Eustoma Andrewsii A. Nels.
{Eustoma Russellianum (Hook.) Griseb.
C. Eustomae Peck
C. nepheloides Ell. & Holw.
Eustoma silenifolium Salisb.
C. nepheloides Ell. & Holw.
Falcata comosa (L.) Kuntze = Amphicarpa monoica (L.) Ell.
Ficus carica L.
C. Bolleana (Thuem.) Speg.
C. Fici Heald & Wolf
C. Ficina Tharp
{Fragaria vesca L.
{Fragaria virginiana Duchesne
C. vexans C. Massal.
Fraxinus sp.
C. Fraxinea Ell. & Ev.
C. Fraxinites Ell. & Ev.
C. lumbricoides Turconi & Maffei
C. superflua Ell. & Holw.
Fraxinus pennsylvanica Marsh
C. texensis Ell. & Gall.
Fraxinus viridis Michx. f. = F. pennsylvanica Marsh
Froelichia floridana (Nutt.) Moq.
C. crassoides Davis
Galactia spp.
C. flagellifera Atk.
C. Galactiae Ell. & Ev.
{Galium Aparine L.
{Galium asprellum Michx.
C. Galii Ell. & Holw.
Galium pilosum Ait.
C. Galii Ell. & Holw.
C. tenuis Peck
{Galium pilosum Ait. var. puncticulosum (Michx.) Torr. & Gray
{Galium tinctorium L.
C. Galii Ell. & Holw.
Galium trifidum Ait.
C. punctoidea Ell. & Holw.
Galium triflorum Michx.
C. Galii Ell. & Holw.
Garrya elliptica Dougl.
C. Garryae Harkn.
C. glomerata Harkn.
Gaultheria procumbens L.
C. Gaultheriae Ell. & Ev.
Gaura biennis L.
C. Gaurae Kell. & Sw.
Gayophytum diffusum Torr. & Gray
C. Gayophyti Ell. & Ev.
Gentiana crinita Froel.
C. gentianicola Ell. & Ev.
Gentiana linearis Froel.
C. Gentianae Peck
{Geranium carolinianum L.
{Geranium maculatum L.
C. Geranii Kell. & Sw.
{Gerardia grandiflora Benth.
{Gerardia punctata Robins.
C. Gerardiae Ell. & Dearn.
Gerardia quercifolia Pursh = G. virginica (L.) BSP.
Gerardia virginica (L.) BSP.
C. clavata (Ger.) Peck
C. Gerardiae Ell. & Dearn.
Gleditsia triacanthos L.
C. condensata Ell. & Kell.
C. olivacea (Berk. & Rav.) Ell.
Glottidium floridanum DC. = Sesbania platycarpa Pers.
Glycine Apios L. = Apios tuberosa Moench
Glycine hispida = G. Max Merr.
Glycine Max Merr.
C. canescens Ell. & Mart.
C. cruenta Sacc.
Glycine Soja Sieb. & Zucc. = G. Max Merr.
Gnaphalium spp.
C. Gnaphaliacea Cooke
Gnaphalium decurrens Ives
C. Gnaphalii Harkn.
{Gnaphalium polycephalum Michx.
{Gnaphalium purpureum L.
C. Gnaphaliacea Cooke

Gomphocarpus cordifolius Benth.
C. Hanseni Ell. & Ev.
Gomphocarpus viridiflorus (Raf.) Spreng. = Acerates viridiflora (Raf.) Eaton
Gonolobus hirsutus Michx. = Vincetoxicum hirsutum (Michx.) Britt.
Gossypium sp.
Gossypium barbadense L.
C. Gossypina Cooke
Gossypium Cavanillesianum Tod.
C. Althaeina Sacc.
Gossypium herbaceum L.
C. Gossypina Cooke
Gossypium hirsutum Cav. = G. Cavanillesianum Tod.
Gratiola pilosa Michx.
C. Gratiolae Ell. & Ev.
Grindelia sp.
Grindelia squarrosa (Pursh) Dunal
C. Grindeliae Ell. & Ev.
Grossularia reclinata (L.) Mill. = Ribes Grossularia L.
Gymnocarpus sp. = Uapaca sp.
Gymnocladus canadensis Lam. = G. dioica (L.) Koch
Gymnocladus dioica (L.) Koch
C. Gymnocladi Ell. & Kell.
Halenia deflexa (Sm.) Griseb.
C. gentianicola Ell. & Ev.
Hamamelis virginiana L.
C. Hamamelidis Ell. & Ev.—N. Am. Fungi, 2586, nomen nudum.
Hedera sp.
C. Ampelopsidis Peck
Helenium microcephalum DC.
C. Helenii Tharp
Helianthus sp.
C. Helianthi Ell. & Ev.
Helianthus annuus L.
C. pachypus Ell. & Kell.
Helianthus doronicoides Lam.
Helianthus hirsutus Raf.
C. Helianthi Ell. & Ev.
Helianthus lenticularis Dougl. = H. annuus L.
Helianthus Maximiliani Schrad.
Helianthus occidentalis Riddell
C. Helianthi Ell. & Ev.
Helianthus petiolaris Nutt.
C. pachypus Ell. & Kell.
Helianthus rigidus Desf. = H. scaberrimus Ell.
Helianthus scaberrimus Ell.
Helianthus strumosus L.
Helianthus tuberosus L.
C. Helianthi Ell. & Ev.
Heliotropium curassavicum L.
C. Heliotropii Ell. & Ev.
Hemerocallis fulva L.
C. Hemerocallis Tehon
Herpetica alata (L.) Raf. = Cassia alata L.
Heteromeles arbutifolia Roem.
C. Heteromeles Harkn.
Heuchera americana L.
C. Heucherae Ell. & Mart.
Hibiscus esculentus L.
C. Althaeina Sacc.
C. brachypoda Speg.
C. Hibisci Tracy & Earle
Hibiscus tiliaceus L.
C. Hibisci Tracy & Earle
C. Hibiscina Ell. & Ev.
Hicoria pecan Britt. = Carya illinoensis (Wang.) K. Koch
Hieracium venosum L.
C. Hieracii Ell. & Ev.
Holcus halepensis L.
Holcus Sorghum L.
C. Sorghi Ell. & Ev.
Houstonia coerulea L.
C. Houstoniae Ell. & Ev.
Hybanthus concolor (Forst.) Spreng.
C. columbiensis Ell. & Ev.
Hydrangea sp.
C. Hydrangeae Ell. & Ev.
C. Hydrangeana Tharp
Hydrangea arborescens L.
C. arborescentis Tehon & Daniels
Hydrocotyle spp.
Hydrocotyle americana L.
Hydrocotyle Canbyi Coult. & Rose
Hydrocotyle interrupta Muhl.
Hydrocotyle umbellata L.
Hydrocotyle verticillata Thunb.
C. Hydrocotyles Ell. & Ev.
Hydrolea ovata Nutt.
C. Namae Dearn. & House

{Hymenocallis sp.
{Hymenocallis caribaea Herb.
C. Amaryllidis Ell. & Ev.
Hymenocallis crassifolia Herb.
C. Pancratii Ell. & Ev.
Hymenocallis declinata Roem. = H. caribaea Herb.
Hypericum adpressum Bart.
C. Hyperici Tehon & Daniels
Hyptis sp.
C. Ellissii Sacc. & Syd.
Ichthyomethia piscipula L. = Piscidia Erythrina L.
Ilex glabra (L.) Gray
C. Ilicis Ell.
Ilex opaca Ait.
C. ilicicola Lieneman, nom. nov.
C. Pulvinula Cooke & Ell.
Ionidium concolor Benth. & Hook. = Hybanthus concolor (Forst.) Spreng.
Ipomoea acetosaefolia Roem. & Schult.
C. sp., acc. to Torr. Bot. Club Bull. **28:** 84. 1901.
{Ipomoea lacunosa L.
{Ipomoea pandurata (L.) Meyer
C. Ipomoeae Wint.
Ipomoea purpurea (L.) Roth.
C. alabamensis Atk.
C. Ipomoeae Wint.
C. viridula Ell. & Ev.
Ipomoea stolonifera (Cyrill.) Poir.
C. Convolvuli Tracy & Earle
Isanthus brachiatus (L.) BSP.
C. Isanthi Ell. & Kell.
Isanthus caeruleus Michx. = I. brachiatus (L.) BSP.
Isopyrum biternatum (Raf.) Torr. & Gray
C. Merrowii Ell. & Ev.
Isopyrum thalictroides L.
The only mention of this host for *C. Merrowii* is Syll. Fung. **11:** 625. 1895.
Jatropha stimulosa Michx.
C. Jatrophae Atk.
{Juglans cinerea L.
{Juglans nigra L.
C. Juglandis Kell. & Sw.
Juniperus communis L. var. alpina Gaud.
C. Sequoiae Ell. & Ev.
Juniperus virginiana L.
C. Sequoiae Juniperi Ell. & Ev.
Jussiaea decurrens (Walt.) DC. = Jussieua decurrens (Walt.) DC.
Jussiaea leptocarpa Nutt. = Jussieua leptocarpa Nutt.
{Jussieua decurrens (Walt.) DC.
{Jussieua leptocarpa Nutt.
C. Jussieuae Atk.
Kalmia latifolia L.
C. Kalmiae Ell. & Ev.
C. sparsa Cooke
Lagenaria vulgaris Ser. = Cucurbita Lagenaria L.
Lagerstroemia indica L.
C. Lythracearum Heald & Wolf
Lathyrus latifolius L.
C. Lathyrina Ell. & Ev.
Lathyrus maritimus (L.) Bigel.
C. Lathyri Dearn. & House
{Lathyrus palustris L.
{Lathyrus venosus Muhl.
C. Viciae Ell. & Holw.
Laurus Benzoin L.
C. Smilacina Sacc.
Leonotis nepetaefolia R. Br.
C. Leonotidis Cooke
Leonotis ovata Boj. = L. nepetaefolia R. Br.
{Lepachys columnaris (Sims) Torr. & Gray
{Lepachys pinnata (Vent.) Torr. & Gray
C. Ratibidae Ell. & Barth.
{Lepidium sp.
{Lepidium campestre (L.) R. Br.
{Lepidium virginicum L.
C. Lepidii Peck
Lespedeza ? sp.
C. flagellifera Atk.
Lespedeza capitata Michx.
C. flagellifera Atk.
C. latens Ell. & Ev.
C. Lespedezae Ell. & Dearn.
Lespedeza frutescens (L.) Britt
C. flagellifera Atk.

Ligustrum sp.
C. *adusta* Heald & Wolf
C. *Ligustri* Roum.
Ligustrum californicum Hort. = Ligustrum ovalifolium Hassk.
Ligustrum japonicum Thunb.
C. *Ligustri* Roum.
Ligustrum ovalifolium Hassk.
C. *adusta* Heald & Wolf
Lilium longiflorum Thunb.
C. *unicolor* Sacc. & Penz.
Linum virginianum L.
C. *Lini* Ell. & Ev.
{Lippia lanceolata Michx.
{Lippia nodiflora (L.) Michx.
C. *Lippiae* Ell. & Ev.
Liquidambar Styraciflua L.
C. *Liquidambaris* Cooke & Ell. U. S. D. A. Bull. 1366. 1926, nomen nudum.
C. *tuberculans* Ell. & Ev.
Liriodendron Tulipifera L.
C. *Liriodendri* Ell. & Harkn.
Litsea geniculata (Walt.) Nicholson
C. *olivacea* (Berk. & Rav.) Ell.
Lobelia amoena Michx.
C. *effusa* (Berk. & Curt.) Ell.
C. *Lobeliae* Kell. & Sw.
{Lobelia cardinalis L.
{Lobelia inflata L.
{Lobelia puberula Michx.
C. *effusa* (Berk. & Curt.) Ell.
Lobelia syphilitica L.
C. *effusa* (Berk. & Curt.) Ell.
C. *Lobeliae* Kell. & Sw.
Lonicera spp.
C. *antipus* Ell. & Holw.
C. *varia* Peck
{Lonicera flava Sims
{Lonicera glaucescens Rydb.
{Lonicera hirsuta Eat.
{Lonicera Sullivantii Gray
C. *antipus* Ell. & Holw.
Ludwigia alternifolia L.
C. *Ludwigiae* Atk.
Lupinus diffusus Nutt.
C. *Lupini* Cooke
Lupinus perennis L.
C. *filispora* Peck
C. *longispora* Peck
Lupinus pilosus L.
C. *longispora* Peck
Lupinus subcarnosus Hook.
C. *lupinicola* Lieneman, nom. nov.
Lupinus texensis Hook. = L. subcarnosus Hook.
Lycium halimifolium Mill.
C. *Lycii* Ell. & Halst.
Lycium vulgare Dunal = L. halimifolium Mill.
Lycopersicum esculentum Mill.
C. *canescens* Ell. & Mart.
C. *cruenta* Sacc.
Lycopus rubellus Moench
C. *Lycopi* Ell. & Ev.
Lysimachia stricta Ait. = L. terrestris (L.) BSP.
Lysimachia terrestris (L.) BSP.
C. *Lysimachiae* Ell. & Halst.
Lythrum alatum Pursh
C. *Lythri* (Westd.) Niessl.
Maclura aurantiaca Nutt. = M. pomifera (Raf.) Schneider
Maclura pomifera (Raf.) Schneider
C. *Maclurae* Ell. & Ev.
Magnolia glauca L. = M. virginiana L.
Magnolia virginiana L.
C. *Magnoliae* Ell. & Harkn.
Maianthemum bifolium DC.
C. *Majanthemi* Fckl.
Maianthemum canadense Desf.
C. *Majanthemi* Fckl.
C. *subsanguinea* Ell. & Ev.
Malachra alcaefolia Jacq. = M. capitata L.
Malachra capitata L.
C. *Malachrae* Heald & Wolf
Malachra rotundifolia Schrank = M. capitata L.
Mallotus japonicus Muell. = Rottlera japonica Spreng.
Malus sylvestris Mill. = Pyrus Malus L.
Malva spp.
C. *Althaeina* Sacc.
Manihot esculenta Crantz = M. utilissima Pohl

Manihot Manihot (L.) Cockerell = M. utilissima Pohl
Manihot utilissima Pohl
  C. Cassavae Ell. & Ev.
Marrubium vulgare L.
  C. Marrubii Tharp
Martynia louisiana Mill.
  C. beticola Sacc.
Medicago arabica Huds.
  C. Medicaginis Ell. & Ev.
Medicago denticulata Willd. = M. hispida Gaertn.
{Medicago hispida Gaertn.
{Medicago lupulina L.
  C. Medicaginis Ell. & Ev.
Medicago maculata Sibth. = M. arabica Huds.
Medicago sativa L.
  C. helvola Sacc. var. *Medicaginis* Chester
  C. Medicaginis Ell. & Ev.
Megapterium Fremontii (Wats.) Britt. = Oenothera Fremontii Wats.
Meibomia grandiflora Kuntze = Desmodium grandiflorum (Walt.) DC.
Meibomia mollis = Desmodium molle DC.
Melia Azedarach L.
  C. leucosticta Ell. & Ev.
  C. Meliae Ell. & Ev.
Melilotus alba Desf.
  C. Davisii Ell. & Ev.
Menispermum canadense L.
  C. Menispermi Ell. & Holw.
Mentha arvensis L. var. canadensis (L.) Briquet
  C. menthicola Tehon & Daniels
Mentha canadensis L. = M. arvensis L. var. canadensis (L.) Briquet
Micrampelis lobata (Michx.) Greene = Echinocystis lobata (Michx.) Torr. & Gray
Mikania scandens (L.) Willd.
  C. Mikaniae Ell. & Ev.
Mimulus alatus Ait.
  C. Mimuli Ell. & Ev.
Mirabilis Jalapa L.
  C. Mirabilis Tharp
Mitreola petiolata Torr. & Gray = Cynoctonum Mitreola (L.) Britt.
Modiola caroliniana (L.) Don
  C. Althaeina Sacc. var. *Modiolae* Atk.
  C. Modiolae Tharp
Modiola multifida Moench = M. caroliniana (L.) Don
Mollugo verticillata L.
  C. molluginicola Lieneman, nom. nov.
  C. Molluginis Halst.
Morongia uncinata Willd. = Schrankia uncinata Willd.
Morus sp.
  C. moricola Cooke
  C. pulvinulata Sacc. & Wint.
Morus alba L.
  C. moricola Cooke
Morus rubra L.
  C. moricola Cooke
  C. pulvinulata Sacc. & Wint.
Muhlenbergia diffusa Willd. = M. Schreberi Gmel.
{Muhlenbergia foliosa Trin.
{Muhlenbergia mexicana (L.) Trin.
{Muhlenbergia Schreberi Gmel.
{Muhlenbergia sylvatica Torr.
  C. Muhlenbergiae Atk.
Myrica carolinensis Mill.
  C. diffusa Ell. & Ev.[1]
Myrica cerifera L.
  C. diffusa Ell. & Ev.[1]
  C. dispersa Ell. & Ev.
  C. Myricae Tracy & Earle
  C. penicillus Ell. & Ev.
Nabalus altissima (L.) Hook = Prenanthes altissima L.
Nabalus aspera (Michx.) Torr. & Gray = Prenanthes aspera Michx.
Nama ovata (Nutt.) Britt. = Hydrolea ovata Nutt.
Nasturtium palustre (L.) DC. = Radicula palustris (L.) Moench
Negundo aceroides Moench = Acer Negundo L.

[1] This species of *Cercospora*, otherwise known on members of the Solanaceae, is reported on this host in the U. S. D. A. Bull. 1366. 1926.

Negundo fraxinifolium Nutt. = Acer Negundo L.
Nelumbo lutea (Willd.) Pers.
 C. Nelumbonis Tharp
Nelumbo luteum Willd. = N. lutea (Willd.) Pers.
Nepeta Cataria L.
 C. Nepetae Tehon
Nerium Oleander L.
 C. neriella Sacc.
Nesaea verticillata HBK. = Decodon verticillatus (L.) Ell.
{Nicotiana repanda Willd.
{Nicotiana Tabacum L.
 C. Nicotianae Ell. & Ev.
Nymphaea (cultivated)
 C. exotica Ell. & Ev.
 C. Nymphaeaceae Cooke & Ell.
Nymphaea odorata Ait. = Castalia odorata (Ait.) Woodville & Wood
Nyssa multiflora Wang. = N. sylvatica Marsh
Nyssa sylvatica Marsh
 C. Nyssae Tharp
Oenothera biennis L.
 C. didymospora Ell. & Barth.
 C. Oenotherae Ell. & Ev.
Oenothera Fremontii Wats.
 C. didymospora Ell. & Barth.
Oenothera laciniata Hill
 C. Oenotherae-sinuatae Atk.
Oenothera sinuata L. = O. laciniata Hill
Onagra biennis Scop. = Oenothera biennis L.
Oryza sativa L.
 C. Oryzae Miyake
{Osmorhiza Claytonia (Michx.) Clarke
{Osmorhiza longistylis (Torr.) DC.
 C. Osmorhizae Ell. & Ev.
{Oxybaphus hirsutus (Pursh) Sweet
{Oxybaphus nyctagineus (Michx.) Sweet
 C. Oxybaphi Ell. & Halst.
Oxydendrum arboreum (L.) DC.
 C. Oxydendri Tracy & Earle
Padus americana (L.) Mill. = Prunus virginiana L.
Paeonia officinalis L.
 C. Paeoniae Tehon & Daniels
 C. variicolor Wint.
Pancratium coronarium LeConte = Hymenocallis crassifolia Herb.
Panicum dichotomum L.
 C. fusimaculans Atk.
Panicum latifolium L.
 C. Panici Davis
Pariti tiliaceum (L.) St. Hil. = Hibiscus tiliaceus L.
Parosela enneandra (Nutt.) Britt. = Dalea enneandra Nutt.
Parthenocissus quinquefolia Planch.
 C. Ampelopsidis Peck
Passiflora sp.
 C. regalis Tharp
Passiflora incarnata L.
 C. biformis Peck
 C. fuscovirens Sacc.
 C. truncatella Atk.
Passiflora lutea L.
 C. fuscovirens Sacc.
Passiflora sexflora Juss.
 C. biformis Peck
Pastinaca sativa L.
 C. Apii Fres.
 C. Pastinacae (Sacc.) Peck
Pelargonium spp.
 C. Brunkii Ell. & Gall.
Peltandra alba Raf. = P. sagittaefolia (Michx.) Morong
Peltandra sagittaefolia (Michx.) Morong
 C. pachyspora Ell. & Ev.
Peltandra virginica (L.) Kunth.
 C. Callae Peck & Clint.
 C. pachyspora Ell. & Ev.
Penthorum sedoides L.
 C. sedoidis Ell. & Ev.
{Pentstemon Cobaea Nutt.
{Pentstemon grandiflorus Nutt.
{Pentstemon hirsutus (L.) Willd.
 C. Pentstemonis Ell. & Kell.
Pentstemon pubescens Soland. = P. hirsutus (L.) Willd.
Pepo foetidissima (HBK.) Britt. = Cucurbita foetidissima HBK.
Persea americana Mill.
 C. sp. Stevenson, Fla. Agr. Sta. Bull. 161: 3–23. 1922; Myc. **15**: 145. 1923; U. S. D. A. Bull. 1366. 1926.
Persea gratissima Gaertn. = P. americana Mill.

Persea palustris (Raf.) Sarg.
C. purpurea Cooke
Persica vulgaris Mill. = Prunus Persica (L.) Sieb. & Zucc.
Persicaria Hydropiper (L.) Opiz. = Polygonum Hydropiper L.
Persicaria punctata (Ell.) Small = Polygonum acre HBK.
Petroselinum hortense Hoffm.
C. Apii Fres.
Petunia hybrida Hort.
C. sp.—mentioned in U. S. D. A. Bull. 1366. 1926.
Petunia parviflora Juss.
C. canescens Ell. & Mart.
Peucedanum graveolens (L.) Benth. & Hook. = Anethum graveolens L.
Peucedanum sativum (L.) Benth. & Hook. = Pastinaca sativa L.
Phaseolus sp.
C. canescens Ell. & Mart.
C. columnaris Ell. & Ev.
C. cruenta Sacc.
C. Phaseolorum Cooke
Phaseolus lunatus L.
C. canescens Ell. & Mart.
C. cruenta Sacc.
C. Phaseolorum Cooke
Phaseolus vulgaris L.
C. canescens Ell. & Mart.
C. cruenta Sacc.
{Philadelphus spp.
{Philadelphus coronarius L.
C. angulata Wint.
Phleum pratense L.
C. graminicola Tracy & Earle
Phlox spp.
C. Phlogina Peck
C. omphakodes Ell. & Holw.
{Phlox amoena Sims
{Phlox divaricata L.
{Phlox floridana Benth.
{Phlox maculata L.
C. omphakodes Ell. & Holw.
Photinia arbutifolia Lindl. = Heteromeles arbutifolia Roem.
Physalis spp.
C. Physalidis Ell.
Physalis heterophylla Nees
C. diffusa Ell. & Ev.
C. Physalidis Ell.
Physalis lanceolata Michx.
C. diffusa Ell. & Ev.
Physalis pubescens L.
C. Physalidis Ell.
Physalis virginiana Mill.
C. physalicola Ell. & Barth.
Physalis virginica Gray = P. virginiana Mill.
{Phytolacca americana L.
{Phytolacca decandra L.
{Phytolacca icosandra L.
C. flagellaris Ell. & Mart.
Piaropus crassipes Raf. = Eichhornia speciosa Kunth
Piaropus crassipes (Mart.) Britt. = Eichhornia speciosa Kunth
Pimpinella integerrima (L.) Gray = Taenidia integerrima (L.) Drude
Piscidia Erythrina L.
C. Ichthyomethiae Dearn. & Barth.
{Plantago lanceolata L.
{Plantago lusitanica L.
{Plantago major L.
C. Plantaginis Sacc.
Plantago Rugelii Decne.
C. Plantaginella Tehon
Platanus occidentalis L.
C. platanicola Ell. & Ev.
Pleiotaenia Nuttallii (DC.) Coult. & Rose = Polytaenia Nuttallii DC.
Podophyllum peltatum L.
C. Podophylli Tehon & Daniels
{Polygala cruciata L.
{Polygala lutea L.[1]
C. grisea Cooke & Ell.
Polygonum spp.
C. Polygonacea Ell. & Ev.

[1] Saccardo (Syll. Fung. **4**: 434. 1886) lists this as a host for *Cercospora minuta* Cooke & Ell., with reference to Grev. **5**: 49. 1876. No such species is listed in that place, but instead is *C. grisea* Cooke & Ell. and only on *Polygala lutea* L. So far as can be determined, Cooke and Ell. never published a *C. minuta* and if regarded as distinct it should be referred to Sacc. for authorship.

Polygonum acre HBK.
  C. Hydropiperis (Thuem.) Speg.
Polygonum aviculare L.
  C. avicularis Wint.
{Polygonum Convolvulus L.
{Polygonum dumetorum L.
  C. Polygonacea Ell. & Ev.
Polygonum erectum L.
  C. avicularis Wint.
{Polygonum Hydropiper L.
{Polygonum pennsylvanicum L.
  C. Hydropiperis (Thuem.) Speg.
Polygonum punctatum Ell. = P. acre HBK.
Polygonum sagittatum L.
  C. avicularis Wint. var. *Sagittati* Atk.
Polygonum scandens L.
  C. Polygonacea Ell. & Ev.
Polypodium Phyllitidis L.
  C. Phyllitidis Hume
Polytaenia Nuttallii DC.
  C. Polytaeniae Ell. & Ev.
Pontederia cordata L.
  C. Pontederiae Ell. & Dearn.
Populus alba L.
  C. Populina Ell. & Ev.
Populus angulata Ait. = P. deltoides Marsh
Populus deltoides Marsh
  C. populicola Tharp
  C. Populina Ell. & Ev.
  C. reducta Syd.
Populus dilatata Ait.
  C. Populina Ell. & Ev.
Populus monilifera Ait. = P. deltoides Marsh
Potentilla palustris (L.) Scop.
  C. Comari Peck
Prenanthes alba L.
  C. brunnea Peck
  C. tabacina Ell. & Ev.
Prenanthes altissima L.
  C. brunnea Peck
  C. effusa (Berk. & Curt.) Ell.
{Prenanthes aspera Michx.
{Prenanthes crepidinea Michx.
  C. Prenanthis Ell. & Kell.
Prosopis glandulosa Torr.
  C. Prosopidis Heald & Wolf
Prunus sp.
  C. rosicola Pass.
Prunus americana Marsh
  C. circumscissa Sacc.
  C. prunicola Ell. & Ev.
Prunus armeniaca L.
  C. circumscissa Sacc.
Prunus Avium L.
  C. Cerasella Sacc.
  C. circumscissa Sacc.
Prunus Cerasus L.
  C. Cerasella Sacc.
  C. rubrotincta Ell. & Ev.
Prunus communis Fritsch
  C. circumscissa Sacc.
Prunus demissa D. Dietr. = P. virginiana L.
{Prunus domestica L.
{Prunus pennsylvanica L.
  C. circumscissa Sacc.
Prunus Persica (L.) Sieb. & Zucc.
  C. circumscissa Sacc.
  C. consobrina Ell. & Ev.
  C. rubrotincta Ell. & Ev.
{Prunus serotina Ehrh.
{Prunus spinosa L.
  C. circumscissa Sacc.
Prunus virginiana L.
  C. Cerasella Sacc.
  C. circumscissa Sacc.
Psedera quinquefolia (L.) Greene
  C. Ampelopsidis Peck
  C. psedericola Tehon
Psoralea argophylla Pursh
  C. latens Ell. & Ev.
Ptelea trifoliata L.
  C. afflata Wint.
  C. Pteleae Wint.
Ptiloria virgata (Benth.) Greene = Stephanomeria virgata Benth.
Punica Granatum L.
  C. Lythracearum Heald & Wolf
Pyrus arbutifolia (L.) L. f.
  C. Pyri Farlow
Pyrus communis L.
  C. minima Tracy & Earle
  C. Pyri Farlow

Pyrus japonica (Pers.) Thunb.
C. Cydoniae Ell. & Ev.
Pyrus Malus L.
C. Mali Ell. & Ev.
Pyrus melanocarpa (Michx.) Willd.
C. Pyri Farlow
Quercus chrysolepis Liebm.
C. macrochaeta Ell. & Ev.
Quercus virens Ait. = Q. virginiana Mill.
Quercus virginiana Mill.
C. polytricha Cooke
Radicula Armoracia (L.) Robins.
C. Armoraciae Sacc.
{Radicula Nasturtium-aquaticum (L.) Britten & Rendle
Radicula palustris (L.) Moench
Radicula sylvestris (L.) Druce
C. Nasturtii Pass.
Rafinesquia californica Nutt.
C. Rafinesquiae Harkn.
{Ranunculus repens L.
Ranunculus septentrionalis Poir.
C. Ranunculi Ell. & Holw.
Raphanus sativus L.
C. atrogrisea Ell. & Ev.
C. Cruciferarum Ell. & Ev.
Ratibida columnaris (Sims) Don = Lepachys columnaris (Sims) Torr. & Gray
Reseda odorata L.
C. Resedae Fckl.
Rhamnus sp.
C. aeruginosa Cooke
{Rhamnus alnifolia L'Her.
Rhamnus cathartica L.
C. Rhamni Fckl.
Rheum Rhaponticum L.
C. Rhapontici Tehon & Daniels
{Rhexia mariana L.
Rhexia virginica L.
C. erythrogena Atk.
Rhus aromatica Ait. = R. canadensis Marsh
Rhus canadensis Marsh
C. Rhuina Cooke & Ell.
Rhus copallina L.
C. Rhuina Cooke & Ell.
C. Rhuina Cooke & Ell. var. *nigromaculans* Peck
{Rhus Cotinus L.
Rhus glabra L.
Rhus hirta (L.) Sudw.
Rhus pumila Michx.
C. Rhuina Cooke & Ell.
Rhus Toxicodendron L.
C. Bartholomaei Ell. & Kell.
C. Rhuina Cooke & Ell.
C. Toxicodendri Ell.
Rhus typhina L. = R. hirta (L.) Sudw.
Rhus venenata DC. = R. Vernix L.
Rhus Vernix L.
C. infuscans Ell. & Ev.
C. Rhuina Cooke & Ell.
Rhynchospora glomerata (L.) Vahl = R. glomerata (L.) Vahl
Ribes sp.
C. Ribis Earle
Ribes aureum Pursh
C. ribicola Ell. & Ev.
Ribes bracteosum Douglas
C. coalescens Davis
Ribes Grossularia L.
C. sp.—mentioned in U. S. D. A. Bull. 1366. 1926.
Ribes sanguineum Pursh
C. ribicola Ell. & Ev.
Ribes tenuiflorum Lindl. = R. aureum Pursh
Ribes vulgare Lam.
C. angulata Wint.
Richardia africana Kunth.
C. richardiaecola Atk.
Richardia scabra St. Hil.
C. Carveriana Sacc. & D. Sacc.
Richardsonia scabra St. Hil. = Richardia scabra St. Hil.
Ricinus communis L.
C. canescens Ell. & Mart.
C. Ricinella Sacc. & Berl.
Ridan alternifolius (L.) Britt. = Actinomeris alternifolia (L.) DC.
Rivina laevis L.
C. flagellaris Ell. & Mart.
Roripa Armoracia (L.) Hitchc. = Armoracia rusticana Gaertn., Mey. & Scherb.

Rosa spp.
C. rosicola Pass.
C. Rosigena Tharp
Rosa arkansana Porter
C. rosicola Pass.
Rosa blanda Ait.
C. rosicola Pass. var. *undosa* Davis
Rosa carolina L.
C. rosicola Pass.
Rosa humilis Marsh
C. rosicola Pass. var. *undosa* Davis
Rottlera japonica Spreng.
C. Malloti Ell. & Ev.
Rubus spp.
C. bliti Tharp
C. Rubi Sacc.
Rubus canadensis L.
C. septorioides Ell. & Ev.
C. Rubi Sacc.
{Rubus cuneifolius Pursh
{Rubus fructicosus L.
{Rubus villosus Ait.
C. Rubi Sacc.
Rudbeckia hirta L.
C. tabacina Ell. & Ev.
Rudbeckia laciniata L.
C. Rudbeckiae Peck
C. tabacina Ell. & Ev.
Rudbeckia triloba L.
C. tabacina Ell. & Ev.
{Ruellia ciliosa Pursh
{Ruellia parviflora (Nees) Britt.
C. consociata Wint.
Rumex Acetosella L.
C. Acetosellae Ell.
Rumex crispus L.
C. Acetosellae Ell. var. *maculosa* Peck
Rynchospora glomerata (L.) Vahl
C. crinospora Atk.
Sabbatia angularis (L.) Pursh
C. Sabbatiae Ell. & Ev.
Saccharum officinarum L.
C. vaginae Kreuger
{Sagittaria heterophylla Pursh
{Sagittaria lancifolia L.
{Sagittaria latifolia Willd.
C. Sagittariae Ell. & Kell.
Sagittaria variabilis Engelm. = S. latifolia Willd.
{Salix spp.
{Salix nigra Marsh
C. Salicina Ell. & Ev.
Salvia farinacea Benth.
C. salviicola Tharp
Sambucus spp.
C. lateritia Ell. & Halst.
Sambucus canadensis L.
C. catenospora Atk.
C. Depazeoides (Desm.) Sacc.
{Sambucus nigra L.
{Sambucus pubens Michx.
{Sambucus racemosa L.
C. lateritia Ell. & Halst.
Sanguinaria canadensis L.
C. Sanguinariae Peck
Sanicula gregaria Bicknell
C. Saniculae Davis
Saururus cernuus L.
C. Saururi Ell. & Ev.
Schrankia uncinata Willd.
C. Morongiae Tracy & Earle
Scutellaria cordifolia Muhl. = S. versicolor Nutt.
Scutellaria versicolor Nutt.
C. Scutellariae Ell. & Ev.
Sechium edule (Jacq.) Sw.
C. Cucurbitae Ell. & Ev.
Sedum sp.
C. Sedi Ell. & Ev.
Selinum Gmelini Bray
C. Apii Fres. var. *Selini-Gmelini* Sacc. & Scalia
Senecio aureus L.
C. Senecionis Ell. & Ev.
Sepium sebiferum (L.) Roxb.
C. Stillingiae Ell. & Ev.
Sequoia gigantea DC.
C. Sequoiae Ell. & Ev.
Sesbania platycarpa Pers.
C. glotidiicola Tracy & Earle
Setaria glauca (L.) Beauv.
C. Setariae Atk.
C. setariicola Tehon & Daniels
C. striaeformis
Sicyos angulatus L.
C. Echinocystis Ell. & Mart.
Sida spinosa L.
C. sidaecola Ell. & Ev.

Sium cicutaefolium Schrank
  C. Sii Ell. & Ev.
{Silphium compositum Michx.
{Silphium integrifolium Michx.
  C. Silphii Ell. & Ev.
Silphium laciniatum L.
  C. Silphii Ell. & Ev. var. *laciniati* Tehon & Daniels
Sisymbrium officinale (L.) Scop.
  C. Cruciferarum Ell. & Ev.
  C. Nasturtii Pass.
Smilacina canadensis Pursh = Maianthemum canadense Desf.
Smilacina sessilifolia Nutt.
  C. Smilacinae Ell. & Ev.
Smilax sp.
  C. nubilosa Ell. & Ev. See note concerning *C. nubilosa.*
Smilax spp.
  C. Smilacis Thuem.
{Smilax aspera L.
{Smilax bona-nox L.
  C. Smilacina Sacc.
Smilax glauca Walt.
  C. Smilacina Sacc.
  C. Smilacis Thuem.
Smilax hispida Muhl.
  C. Smilacis Thuem.
Smilax laurifolia L.
  C. Smilacina Sacc.
{Smilax rotundifolia L.
{Smilax tamnifolia Michx.
  C. Smilacis Thuem.
Soja max (L.) Moench = Glycine Max Merr.
Solanum carolinense L.
  C. atromarginalis Atk.
  C. carolinensis Tharp
Solanum Dulcamara L.
  C. Dulcamarae (Peck) Ell.
Solanum nigrum L.
  C. atromarginalis Atk.
  C. nigri Tharp
  C. rigospora Atk.
Solanum tuberosum L.
  C. concors (Casp.) Sacc.
  C. solanicola Atk.
{Solidago latifolia L.
{Solidago serotina Ait.
  C. stomatica Ell. & Davis
Sophronanthe pilosa (Michx.) Small = Gratiola pilosa Michx.
Sorghum halepensis (L.) Pers. = Holcus halepensis L.
Sorghum vulgare Pers. = Holcus Sorghum L.
Spathyema Foetida (L.) Raf. = Symplocarpus foetidus (L.) Nutt.
Spermacoce ocymoides Burm. = Borreria micrantha Torr. & Gray
Spinacia oleracea L.
  C. beticola Sacc.
  C. dubia (Riess) Wint.
  C. flagelliformis Ell. & Halst.
Spiraea aruncus L.
  C. sp.—Wisc. Acad. Trans. **15:** 779. 1907.
{Spiraea sp.
{Spiraea salicifolia L.
  C. Rubigo Cooke & Harkn.
Sporobolus asper (Michx.) Kunth
  C. seriata Atk.
Stachys palustris L.
  C. Stachydis Ell. & Ev.
Stephanomeria virgata Benth.
  C. clavicarpa Ell. & Ev.
Stillingia sebifera Michx. = Sepium sebiferum (L.) Roxb.
Stizolobium Deeringianum Bort.
  C. Mucunae Syd. U. S. D. A. Bull. 1366. 1926.
  C. Stizolobii Syd. U. S. D. A. Bull. 1366. 1926.
Streptopus amplexifolius (L.) DC.
  C. Streptopi Dearn. & Barth.
Stylisma humistrata (Walt.) Chapm. = Breweria humistrata (Walt.) Gray
Stylosanthes biflora (L.) BSP.
  C. Commonsii Sacc.
Stylosanthes elatior Sw. = S. biflora (L.) BSP.
Symphoricarpos orbiculatus Moench
  C. Symphoricarpi Ell. & Ev.
Symphoricarpos vulgaris Michx. = S. orbiculatus Moench

Symplocarpus foetidus (L.) Nutt.
C. Symplocarpi Peck
Syringa sp.
C. macromaculans Heald & Wolf
Syringa persica L.
C. lilacis (Desm.) Sacc.
Taenidia integerrima (L.) Drude
C. platyspora Ell. & Holw.
Tagetes patula L.
C. tageticola Ell. & Ev.
Tecoma radicans (L.) Juss. = Campsis radicans (L.) Seem.
Tephrosia hispidula (Michx.) Pers.
C. Tephrosiae Atk.
Tetranthera geniculata Nees = Litsea geniculata (Walt.) Nicholson
Teucrium canadense L.
C. ferruginea Fckl.
C. racemosa Ell. & Mart.
C. Teucrii Ell. & Kell.
Thalia dealbata Roscoe
C. Thaliae Ell. & Langl.
{Thalictrum dasycarpum Fisch. & Lall.
{Thalictrum dioicum L.
C. fingens Davis
Thermopsis "arenaria." Probably error for "arenosa" Nels.
C. Thermopsidis Earle
{Tilia americana L.
{Tilia cordata Mill.
C. microsora Sacc.
Tilia europaea L. = T. cordata Mill.
Tiniaria convolvulus (L.) Webb. & Mod. = Polygonum Convolvulus L.
Tiniaria dumetorum (L.) Opiz. = Polygonum dumetorum L.
Tithymalopsis corollata (L.) Kl. & Garcke = Euphorbia corollata L.
Toxylon pomiferum Raf. = Maclura pomifera (Raf.) Schneider
Tracaulon sagittatum (L.) Small = Polygonum sagittatum L.
Trachelospermum difforme (Walt.) Gray
C. repens Ell. & Ev.
Tragia nepetaefolia Cav.
C. euphorbiaecola Atk. var. *tragiae* Tharp
Tragopogon porrifolius L.
C. Tragopogonis Ell. & Ev.
{Trifolium agrarium L.
{Trifolium dubium Sibth.
{Trifolium hybridum L.
C. zebrina Pass.
Trifolium incarnatum L.
C. Medicaginis Ell. & Ev.
Trifolium medium L.
C. zebrina Pass.
Trifolium pratense L.
C. Medicaginis Ell. & Ev.
C. zebrina Pass.
Trifolium repens L.
C. helvola Sacc.
C. zebrina Pass.
Tropaeolum majus L.
C. Tropaeoli Atk.
Uapaca sp.
C. inquinans Cooke
Ulmus spp.
C. sphaeriaeformis Cooke
Unifolium canadense (Desf.) Greene = Maianthemum canadense Desf.
Vagnera sessilifolia (Nutt.) Greene = *Smilacina sessilifolia* Nutt.
Verbascum Thapsus L.
C. verbascicola Ell. & Ev.
Verbena sp.
C. papillosa Atk.
Verbena caroliniana Michx.
C. septatissima Tracy & Earle
C. verbenicola Ell. & Ev.
Verbena stricta Vent.
C. Verbenae-strictae Peck
Verbena Xutha Lehm.
C. verbenicola Ell. & Ev.
Verbesina texana Buckl.
C. fulvella Heald & Wolf
Vernonia angustifolia Michx.
C. Vernoniae Ell. & Kell.
Vernonia Baldwini Torr.
C. oculata Ell. & Kell.
C. Vernoniae Ell. & Kell.
Vernonia fasciculata Michx.
C. Vernoniae Ell. & Kell.
Vernonia noveboracensis (L.) Willd.
C. noveboracensis Ell. & Ev.
C. Vernoniae Ell. & Kell.
Veronica scutellata L.
C. tortipes Davis

{Viburnum acerifolium L.
Viburnum cassanoides L.
Viburnum Lentago L.
Viburnum Opulus L.}
C. varia Peck
Viburnum plicatum
C. tinea Sacc., or less probably *C. varia* Peck.
Viburnum pubescens (Ait.) Pursh
C. varia Peck
{Vicia caroliniana Walt.
Vicia sativa L.}
C. Viciae Ell. & Holw.
Vigna Catjang Walp. = Vigna sinensis (L.) Endl.
Vigna luteola (Jacq.) Benth.
C. Vignae Ell. & Ev.
Vigna sinensis (L.) Endl.
C. canescens Ell. & Mart.
C. cruenta Sacc.
C. Dolichi Ell. & Ev.
C. Vignae Ell. & Ev.
Vigna unguiculata (L.) Walp. = Vigna sinensis (L.) Endl.
Vincetoxicum spp.
C. Bellynckii (Westd.) Sacc.
Vincetoxicum hirsutum (Michx.) Britt.
C. Vincetoxici Ell. & Ev.
{Viola blanda Willd.
Viola conspersa Reichenb.}
C. Violae Sacc.
Viola cucullata Ait.
C. granuliformis Ell. & Holw.
C. murina Ell. & Kell.
C. Violae Sacc.
{Viola obliqua, of recent authors, not Hill
Viola odorata L.}
C. Violae Sacc.
Viola sagittata Ait.
C. granuliformis Ell. & Holw.
Viola tricolor L.
C. Violae Sacc.
Viola villosa of recent authors = Viola hirsutula Brainerd
{Vitis sp.
Vitis cordifolia Michx.}
C. Vitis (Lév.) Sacc.
Vitis hederacea Ehrh.
C. psedericola Tehon
C. Ampelopsidis Peck
Vitis indivisa Willd. = Cissus Ampelopsis Pers.
Vitis labruscae L.
C. Vitis (Lév.) Sacc.
Vitis rotundifolia Michx.
C. brachypus Ell. & Ev.
C. Vitis (Lév.) Sacc.
Vitis vulpina L.
C. vulpinae Ell. & Kell.
C. Vitis (Lév.) Sacc.
Vitex Agnus-castus L.
C. Viticis Ell. & Ev.
Washingtonia longistylis (Torr.) Britt. = Osmorhiza longistylis (Torr.) DC.
Weigela sp. = Diervilla sp.
Xanthium spp.
C. xanthicola Heald & Wolf
Xanthoxylum "carolinense" (error for "carolinianum" Lam. ?) = Zanthoxylum Clava-Herculis L.
Xyris elata Chapm.
C. Xyridis Miles
{Yucca filamentosa L.
Yucca gloriosa L.}
C. concentrica Cooke & Ell.
Yucca rupicola Scheele
C. floricola Heald & Wolf
Zanthoxylum Clava-Herculis L.
C. Xanthoxyli Cooke
Zea Mays L.
C. Sorghi Ell. & Ev.
C. Zeae-Maydis Tehon & Daniels
Zinnia sp.
C. atricincta Heald & Wolf
Zinnia elegans Jacq.
C. atricincta Heald & Wolf
C. Zinniae Ell. & Mart.
{Zinnia multiflora L.
Zinnia pauciflora L.}
C. Zinniae Ell. & Mart.
{Zizia aurea (L.) Koch
Zizia cordata (Walt.) DC.}
C. Ziziae Ell. & Ev.
Zizia integerrima (L.) DC. = Taenidia integerrima (L.) Drude

Index of Species of Cercospora

1. *C. Absinthii* (Peck) Sacc. Syll. Fung. **4**: 444. 1886; N. Y. Mus. Rept. **30**: 54. 1878, as *Helminthosporium Absinthii* Peck; Wisc. Acad. Trans. **18**: 269. 1915.
2. *C. Abutilonis* Tehon & Daniels, Myc. **17**: 246. 1925.
3. *C. Acalyphae* Peck, N. Y. Mus. Rept. **34**: 48. 1881; Syll. Fung. **4**: 457. 1886; Jour. Myc. **1**: 20. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 46. 1892; N. J. Agr. Sta. Bull. 313: 128. 1917.
4. *C. Acalypharum* Tharp, Myc. **9**: 106. 1917.
5. *C. Acetosellae* Ell. Torr. Bot. Club Bull. **8**: 65. 1881; Syll. Fung. **4**: 454. 1886; Jour. Myc. **1**: 54. 1885.
6. *C. Acetosellae* Ell. var. *maculosa* Peck, N. Y. Mus. Rept. **40**: 64. 1887.
7. *C. Acnidae* Ell. & Ev. Acad. Phila. Proc. **1891**: 89. 1891; Syll. Fung. **10**: 637. 1892.
8. *C. adusta* Heald & Wolf, Myc. **3**: 14. 1911; B. P. I. Bull. 226: 77. 1912.
9. *C. aeruginosa* Cooke, Hedw. **17**: 39. 1878; Syll. Fung. **4**: 466. 1886; Jour. Myc. **1**: 39. 1885.
10. *C. Aesculina* Ell. & Kell. Jour. Myc. **9**: 105. 1903; Syll. Fung. **18**: 598. 1906.
11. *C. afflata* Wint. Hedw. **24**: 201. 1885; Syll. Fung. **4**: 465. 1886; Jour. Myc. **1**: 125. 1885.
12. *C. Ageratoides* Ell. & Ev. Jour. Myc. **5**: 71. 1889; Syll. Fung. **10**: 627. 1892; Wisc. Acad. Trans. **18**: 269. 1915; *l. c.* **19**: 675. 1919; N. J. Agr. Sta. Bull. 313: 128. 1917.
13. *C. Agrostidis* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 44. 1892; Syll. Fung. **10**: 656. 1892.
14. *C. alabamensis* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 51. 1892; Syll. Fung. **10**: 632. 1892.
15. *C. Alismatis* Ell. & Holw. Jour. Myc. **1**: 63. 1885; Syll. Fung. **4**: 478. 1886.
16. *C. Alternantherae* Ell. & Langl. Jour. Myc. **6**: 36. 1890; Syll. Fung. **10**: 637. 1892.
17. *C. Althaeina* Sacc. Michelia **1**: 269. 1878; Am. Nat. **16**: 810. 1882, as *C. malvicola* Ell. & Mart.; Syll. Fung. **4**: 440. 1886; Jour. Myc. **1**: 38. 1885; *l. c.* **4**: 28. 1888; *l. c.* **8**: 57. 1902; Elisha Mitchell Sci. Soc. Jour. **8**: 60. 1892; B. P. I. Bull. 226: 86. 1912; N. J. Agr. Sta. Bull. 313: 128. 1917.
18. *C. Althaeina* Sacc. var. *Modiolae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 60. 1892.
19. *C. Althaeina* Sacc. var. *praecincta* Davis, Wisc. Acad. Trans. **18**: 260. 1915.
20. *C. Amaryllidis* Ell. & Ev. Jour. Myc. **3**: 14. 1887; Syll. Fung. **10**: 653. 1892.
21. *C. Ammanniae* Tharp, Myc. **9**: 107. 1917.
22. *C. Ampelopsidis* Peck, N. Y. Mus. Rept. **30**: 55. 1876; Grev. **12**: 30. 1883, as *C. pustula* Cooke; Syll. Fung. **4**: 459. 1886; Jour. Myc. **1**: 55. 1885, as *C. pustula* Cooke; Syll. Fung. **4**: 458. 1886, as *C. pustula* Cooke; B. P. I. Bull. 226: 80. 1912, as *C. pustula* Cooke; Myc. **16**: 140. 1924.
23. *C. Anethi* Sacc. Nuovo Giorn. Bot. Ital. **23**: 219. 1916.
24. *C. angulata* Wint. Hedw. **24**: 202. 1885; Syll. Fung. **4**: 459. 1886; Jour. Myc. **1**: 124. 1885.
25. *C. anomala* Ell. & Halst. Jour. Myc. **4**: 8. 1888; Syll. Fung. **10**: 628. 1892.

26. *C. anthelmintica* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 49. 1892; Syll. Fung. **10**: 636. 1892; N. J. Agr. Sta. Bull. 313: 128. 1917.
27. *C. antipus* Ell. & Holw. Jour. Myc. **1**: 5. 1885; Syll. Fung. **4**: 469. 1886; Jour. Myc. **1**: 20. 1885; Wisc. Acad. Trans. **17**: 894. 1914; *l. c.* **21**: 278. 1924; Myc. **16**: 125. 1924.
28. *C. Apii* Fres. Beitr. Myk. 91. 1863; Syll. Fung. **4**: 442. 1886; Jour. Myc. **1**: 36. 1885; N. J. Agr. Sta. Bull. 313: 130. 1917; N. J. Agr. Sta. Rept. **37**: 594. 1917; Mich. Agr. Sta. Tech. Bull. 63. 1923.
29. *C. Apii* Fres. var. *Angelicae* Sacc. & Scalia, Harriman Alaska Exped. **5**: 16. 1904; Syll. Fung. **18**: 602. 1906.
30. *C. Apii* Fres. var. *Selini-Gmelini* Sacc. & Scalia, Harriman Alaska Exped. **5**: 16. 1904; Syll. Fung. **18**: 602. 1906.
31. *C. Apiifoliae* Tharp, Myc. **9**: 107. 1917.
32. *C. Apocyni* Ell. & Kell. Torr. Bot. Club Bull. **11**: 121. 1884; Syll. Fung. **4**: 451. 1886; Jour. Myc. **1**: 62. 1885.
33. *C. Aquilegiae* Kell. & Sw. Jour. Myc. **5**: 74. 1889; Syll. Fung. **10**: 618. 1892.
34. *C. Arborescentis* Tehon & Daniels, Myc. **17**: 246. 1925.
35. *C. arboriae* Tharp, Myc. **9**: 108. 1917.
36. *C. Arcti-Ambrosiae* Halst. Torr. Bot. Club Bull. **20**: 25. 1893.
37. *C. Arctostaphyli* Davis, Wisc. Acad. Trans. **18**: 268. 1915.[1]
38. *C. Argythamniae* Dearn. & House, N. Y. Mus. Bull. 179: 33. 1915.
39. *C. Armoraciae* Sacc. Nuovo Giorn. Bot. Ital. **8**: 188. 1876; Syll. Fung. **4**: 433. 1886; Hedw. **16**: 123. 1877; N. J. Agr. Sta. Bull. 313: 130. 1917.
40. *C. Asclepiodorae* Ell. & Kell. Jour. Myc. **4**: 6, 29. 1888; Syll. Fung. **10**: 635. 1892.
41. *C. Asiminae* Ell. & Kell. Jour. Myc. **3**: 103. 1887; Syll. Fung. **10**: 638. 1892.
42. *C. Asparagi* Sacc. Michelia **1**: 88. 1877; Syll. Fung. **4**: 477. 1886; B. P. I. Bull. 226: 34. 1912.
43. *C. Asterata* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 50. 1892; Syll. Fung. **10**: 627. 1892.
44. *C. atra* Ell. & Ev. Jour. Myc. **4**: 4. 1888; Syll. Fung. **10**: 648. 1892.
45. *C. atricincta* Heald & Wolf, Myc. **3**: 14. 1911; B. P. I. Bull. 226: 89. 1912.
46. *C. atrogrisea* Ell. & Ev. Acad. Phila. Proc. **1893**: 464. 1893; Syll. Fung. **11**: 625. 1895.
47. *C. atromaculans* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 644. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 56. 1892.
48. *C. atromarginalis* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 59. 1892; Syll. Fung. **10**: 635. 1892; B. P. I. Bull. 226: 96. 1912.
49. *C. aurantia* Heald & Wolf, Myc. **3**: 15. 1911; B. P. I. Bull. 226: 27. 1912.
50. *C. avicularis* Wint. Hedw. **24**: 202. 1885; Jour. Myc. **1**: 125. 1885; Syll. Fung. **4**: 455. 1886; Ind. Acad. Proc. **1921**: 146. 1922; Wisc. Acad. Trans. **16**: 758. 1909; **17**: 891. 1914.
51. *C. avicularis* Wint. var. *Sagittati* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 48. 1892.
52. *C. Baccharidis* Ell. & Ev. Acad. Phila. Proc. **1894**: 379. 1894; Syll. Fung. **11**: 627. 1895.

[1] In *l. c.* **21**: 253. 1924, Davis says "*Cercospora arctostaphyli* Davis (Trans. Wis. Acad. **18**: 268) seems to have been founded upon a misapprehension. There is no specimen in the University of Wisconsin herbarium and the characters ascribed are those of *Cercospora gaultheriae* E. & E. It should be stricken out."

53. *C. Bartholomaei* Ell. & Kell. Jour. Myc. **5**: 144. 1889; Syll. Fung. **10**: 639. 1892.
54. *C. Bellynckii* (Westd.) Sacc. Hedw. **15**: 1. 1876; Acad. Roy. Sci. Belgique Bull. **21**²: 240. 1854, as *Cladosporium Bellynckii* Westd.; Syll. Fung. **4**: 450. 1886; B. P. I. Bull. 226: 103. 1912.
55. *C. beticola* Sacc. Nuovo Giorn. Bot. Ital. **8**: 189. 1876; Syll. Fung. **4**: 456 1886; Jour. Myc. **1**: 20. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 46. 1892; B. P. I. Bull. 226: 38, 43. 1912; N. J. Agr. Sta. Bull. 313: 130. 1912; Phytopath. **8**: 135. 1918.
56. *C. Bidentis* Tharp, Myc. **9**: 108. 1917.
57. *C. biformis* Peck, Torr. Bot. Club Bull. **36**: 156. 1909; Syll. Fung. **22**: 1414. 1913.
58. *C. bliti* Tharp, Myc. **9**: 108. 1917; *l. c.* **16**: 139. 1924.
59. *C. Bloxami* Berk. & Br. Ann. Mag. Nat. Hist. V, **9**: 183. 1882; Syll. Fung. **4**: 433. 1886; B. P. I. Bull. 226: 38. 1912.
60. *C. Boehmeriae* Peck, N. Y. Mus. Rept. **34**: 48. 1881; Syll. Fung. **4**: 457. 1886; Jour. Myc. **1**: 37. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 54. 1892; Myc. **18**: 31. 1926.
61. *C. Bolleana* (Thuem.) Speg. Michelia **1**: 475. 1879; Oest. Bot. Zeitschr. **27**: 12. 1877, as *Septosporium Bolleanum* Thuem.; Syll. Fung. **4**: 475. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 61. 1892.
62. *C. Borreriae* Ell. & Ev. Acad. Phila. Proc. **1894**: 379. 1894; Syll. Fung. **11**: 627. 1895.
63. *C. brachiata* Ell. & Ev. Jour. Myc. **4**: 5. 1888; Syll. Fung. **10**: 637. 1892; B. P. I. Bull. 226: 99. 1912.
64. *C. brachypoda* Speg. Anal. Soc. Cient. Arg. **13**: 28. 1882; Syll. Fung. **4**: 441. 1886; U. S. D. A. Bull. 1366. 1926.
65. *C. brachypus* Ell. & Ev. Jour. Myc. **8**: 71. 1902; Syll. Fung. **18**: 598. 1906.
66. *C. Briareus* Ell. & Ev. Acad. Phila. Proc. **1894**: 381. 1894; Syll. Fung. **11**: 629. 1895.
67. *C. Brunkii* Ell. & Gall. Jour. Myc. **6**: 33. 1890; Syll. Fung. **10**: 620. 1892.
68. *C. brunnea* Peck, Torr. Bot. Club Bull. **36**: 156. 1909; Syll. Fung. **22**: 1427. 1913; Wisc. Acad. Trans. **21**: 289. 1924.
69. *C. caespitosa* Ell. & Ev. Acad. Phila. Proc. **1891**: 88. 1891; Syll. Fung. **10**: 657. 1892.
70. *C. Callae* Peck & Clint. N. Y. Mus. Rept. **29**: 52. 1878; Syll. Fung. **4**: 478. 1886; Jour. Myc. **1**: 22. 1885; *l. c.* **4**: 6. 1888; Wisc. Acad. Trans. **14**: 95. 1903; *l. c.* **20**: 400. 1922.
71. *C. Callicarpae* Cooke, Grev. **6**: 140. 1878; Syll. Fung. **4**: 470. 1886; Jour. Myc. **1**: 50. 1885; Iowa Acad. Proc. **7**: 162. 1899.
72. *C. Camptosori* Davis, Wisc. Acad. Trans. **18**: 267. 1915.
73. *C. canescens* Ell. & Mart. Am. Nat. **16**: 1003. 1882; Syll. Fung. **4**: 435. 1886; Jour. Myc. **1**: 21. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 48. 1892; Tuskegee Sta. Bull. **4**: 5. 1904; Jour. Myc. **8**: 73. 1902; N. J. Agr. Sta. Bull. 313: 132. 1917; B. P. I. Bull. 226: 37. 1912.
74. *C. capitati* Tharp, Myc. **9**: 108. 1917.
75. *C. capreolata* Ell. & Ev. Jour. Myc. **8**: 70. 1902; Syll. Fung. **18**: 604. 1906.
76. *C. Capsici* Heald & Wolf, Myc. **3**: 15. 1911; B. P. I. Bull. 226: 42. 1912.
77. *C. Caricina* Ell. & Dearn. Can. Inst. Proc. **1**: 91. 1897; Syll. Fung. **14**: 1105. 1899; Wisc. Acad. Trans. **14**: 96. 1903; *l. c.* **16**: 751. 1909; *l. c.* **17**: 890. 1914; *l. c.* **18**: 86, 100. 1915; *l. c.* **21**: 253, 294. 1924.

78. *C. Caricis* Dearn. & House, N. Y. Mus. Bull. 188: 29. 1916.
79. *C. carolinensis* Tharp, Myc. **9**: 109. 1917.
80. *C. Carveriana* Sacc. & D. Sacc. Syll. Fung. **18**: 607. 1906; Jour. Myc. **8**: 72. June 30, 1902, as *C. Richardsoniae* Ell. & Ev., not *C. Richardsoniae* P. Henn. Hedw. **41**: 117. June 23, 1902.
81. *C. Cassavae*[1] Ell. & Ev. Torr. Bot. Club Bull. **22**: 438. 1895; Syll. Fung. **14**: 1104. 1899.
82. *C. Catalpae* Wint. Hedw. **24**: 203. 1885; Syll. Fung. **4**: 470. 1886; Jour. Myc. **1**: 124. 1885; Tex. Agr. Sta. Bull. **9**: 24. 1890; B. P. I. Bull. 226: 62. 1912.
83. *C. catenospora* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 66. 1892; Syll. Fung. **10**: 645. 1892; B. P. I. Bull. 226: 65. 1912.
84. *C. caulicola* Wint. Hedw. **24**: 203. 1885; Syll. Fung. **4**: 477. 1886; Jour. Myc. **1**: 125. 1885.
85. *C. Caulophylli* Peck, N. Y. Mus. Rept. **33**: 30. 1880; Syll. Fung. **4**: 433. 1886; Jour. Myc. **1**: 39. 1885; *l. c.* **9**: 171. 1903.
86. *C. Ceanothi* Kell. & Sw. Jour. Myc. **4**: 94. 1888; Syll. Fung. **10**: 646. 1892.
87. *C. Cephalanthi* Ell. & Kell. Torr. Bot. Club Bull. **11**: 121. 1884; Syll. Fung. **4**: 466. 1886; *l. c.* **10**: 645. 1892; Jour. Myc. **1**: 22. 1885; *l. c.* **4**: 5. 1888; Elisha Mitchell Sci. Soc. Jour. **8**: 67. 1892.
88. *C. Cerasella* Sacc. Michelia **1**: 266. 1878; Syll. Fung. **4**: 460. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 41. 1892.
89. *C. cercidicola* Ell. Am. Nat. **16**: 810. 1882; Syll. Fung. **4**: 463. 1886; Jour. Myc. **1**: 36. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 42. 1892; B. P. I. Bull. 226: 77. 1912; N. J. Agr. Sta. Bull. 313: 132. 1917.
90. *C. cercidicola* Ell. var. *coremioides* Tehon, Myc. **16**: 140. 1924.
91. *C. Chamaecristae* Ell. & Kell. Jour. Myc. **4**: 7. 1888; Syll. Fung. **10**: 641. 1892.
92. *C. Chionanthi* Ell. & Ev. Field Mus. Bot. Ser. Rept. **1**: 94. 1896; Syll. Fung. **14**: 1103. 1899; N. J. Agr. Sta. Bull. 313: 132. 1917.
93. *C. Chrysanthemi* Heald & Wolf, Myc. **3**: 15. 1911; B. P. I. Bull. 226: 85. 1912.
94. *C. Chrysobalani* Ell. & Ev. Torr. Bot. Club Bull. **22**: 438. 1895; Syll. Fung. **14**: 1101. 1899.
95. *C. Cichorii* Davis, Wisc. Acad. Trans. **19**: 715. 1919.
96. *C. Cinchonae* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 645. 1892.
97. *C. circumscissa* Sacc. Nuovo Giorn. Bot. Ital. **8**: 189. 1876; Hedw. **24**: 203. 1885, as *C. graphioides* Ell.; Syll. Fung. **4**: 460. 1886; Jour. Myc. **1**: 23. 1885; *l. c.* **7**: 66–77. 1892; N. J. Agr. Sta. Bull. 313: 134. 1917; Wisc. Acad. Trans. **19**: 694. 1919.
98. *C. Cirsii* Ell. & Ev. Acad. Phila. Proc. **1894**: 379. 1894; Syll. Fung. **11**: 628. 1895.
99. *C. Citrullina* Cooke, Grev. **12**: 31. 1883; Syll. Fung. **4**: 452. 1886; Jour. Myc. **1**: 20. 1885; B. P. I. Bull. 226: 45. 1912; N. J. Agr. Sta. Bull. 313: 132. 1917.

[1] E. W. Mason in 'Annotated Account of Fungi Received at the Imperial Bureau of Mycology,' Kew, Dec. 31, 1928, makes *C. Cassavae* Ell. & Ev. and *C. manihotis* P. Henn. synonyms of *C. Henningsii* Allesch.

100. *C. clavata* (Ger.) Peck, N. Y. Mus. Rept. **34**: 48. 1881; Torr. Bot. Club Bull. **5**: 27. 1874, as *Helminthosporium clavatum* Ger.; Syll. Fung. **4**: 451. 1886; Jour. Myc. **1**: 54. 1885; *l. c.* **4**: 28. 1888; Wisc. Acad. Trans. **9**: 166. 1893; *l. c.* **17**: 893. 1914; *l. c.* **20**: 416. 1922; *l. c.* **21**: 294. 1924; Myc. **7**: 41. 1915; N. J. Agr. Sta. Bull. 313: 134. 1917.

101. *C. clavicarpa* Ell. & Ev. Erythea **2**: 26. 1894; Syll. Fung. **11**: 628. 1895.

102. *C. Cleomis* Ell. & Halst. Jour. Myc. **6**: 34. 1890; Syll. Fung. **10**: 621. 1892.

103. *C. Clitoriae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 62. 1892; Syll. Fung. **10**: 641. 1892; Iowa Acad. Proc. **7**: 162. 1899.

104. *C. coalescens* Davis, Wisc. Acad. Trans. **15**: 780. 1907.

105. *C. coffeicola* Berk. & Curt. Grev. **9**: 99. 1881; Syll. Fung. **4**: 472. 1886; Jour. Myc. **4**: 5. 1888; Syll. Fung. **10**: 645. 1892.

106. *C. Coleosanthi* Ell. & Ev. Torr. Bot. Club Bull. **24**: 474. 1897; Syll. Fung. **14**: 1102. 1899.

107. *C. Coleroides* Sacc. Jour. Myc. **12**: 252. 1906; Syll. Fung. **22**: 1416. 1913.

108. *C. columbiensis* Ell. & Ev. Jour. Myc. **3**: 15. 1887; Syll. Fung. **10**: 619. 1892.

109. *C. columnaris*[1] Ell. & Ev. Acad. Phila. Proc. **1894**: 380. 1894; Syll. Fung. **11**: 625. 1895.

110. *C. Comandrae* Ell. & Dearn. Acad. Phila. Proc. **1891**: 90. 1891; Syll. Fung. **10**: 637. 1892; Wisc. Acad. Trans. **18**: 267. 1915.

111. *C. Comari* Peck, N. Y. Mus. Rept. **38**: 101. 1885; Syll. Fung. **4**: 440. 1886; Jour. Myc. **1**: 63. 1885.

112. *C. Commonsii* Sacc. Syll. Fung. **10**: 623. 1892; Jour. Myc. **3**: 13. 1887, as *C. Stylosanthis* Ell. & Ev., not *C. Stylosanthis* Speg. Guar. **1**: 169. 1886.

113. *C. concentrica* Cooke & Ell. Grev. **5**: 90. 1877; *l. c.* **7**: 35. 1878, as *C. Yuccae* Cooke; Syll. Fung. **4**: 479. 1886; Jour. Myc. **1**: 23. 1885, as *C. Yuccae* Cooke.

114. *C. concors* (Casp.) Sacc. Syll. Fung. **4**: 449. 1886; K. Akad. Wiss. Berlin Monatsber. **1855**: 314. 1855, as *Fusisporium concors* Casp.

115. *C. condensata* Ell. & Kell. Jour. Myc. **1**: 2. 1885; Syll. Fung. **4**: 438, 462. 1886; Jour. Myc. **2**: 2. 1886; Wisc. Acad. Trans. **18**: 267. 1915.

116. *C. confluens* Lieneman, nom. nov.
(*C. Crataegi* Heald & Wolf, Myc. **3**: 16. 1911, not *C. Crataegi* Sacc. & Massal. Ann. Myc. **3**: 515. 1905; B. P. I. Bull. 226: 70. 1912.)

117. *C. consobrina* Ell. & Ev. Jour. Myc. **3**: 19. 1887; Syll. Fung. **10**: 643. 1892.

118. *C. consociata* Wint. Hedw. **22**: 70. 1883; Syll. Fung. **4**: 470. 1886; Jour. Myc. **1**: 53. 1885; Ala. Agr. Sta. Bull. 80: 144. 1897; Iowa Acad. Proc. **7**: 163. 1899.

119. *C. conspicua* Earle, N. Y. Bot. Gard. Bull. **3**: 312. 1905; Syll. Fung. **18**: 596. 1906.

120. *C. Convolvuli* Tracy & Earle, Torr. Bot. Club Bull. **28**: 187. 1901; Syll. Fung. **18**: 605. 1906.

121. *C. Corni* Davis, Wisc. Acad. Trans. **18**: 268. 1915; *l. c.* **19**: 675. 1919.

122. *C. cornicola* Tracy & Earle, Torr. Bot. Club Bull. **23**: 205. 1896; Syll. Fung. **14**: 1101. 1899; B. P. I. Bull. 226: 65. 1912.

123. *C. crassa* Sacc. Michelia **1**: 88. 1877; Syll. Fung. **4**: 448. 1886; Wisc. Acad. Trans. **19**: 689. 1919, as *Alternaria crassa* (Sacc.) Rands.

[1] Dr. L. O. Overholts, in an article now in manuscript, shows *C. columnaris* Ell. and Ev. to be synonymous with *Isariopsis griseola* Sacc.

124. *C. crassoides* Davis, Wisc. Acad. Trans. **21**: 298. 1924.
125. *C. crinospora* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 58. 1892; Syll. Fung. **10**: 655. 1892.
126. *C. crotonicola* Ell. & Barth. Jour. Myc. **8**: 177. 1902; Syll. Fung. **18**: 602. 1906.
127. *C. crotonifolia* Cooke, Grev. **12**: 31. 1883; Syll. Fung. **4**: 473. 1886; Jour. Myc. **1**: 21. 1885.
128. *C. Crotonis* Ell. & Ev. Acad. Phila. Proc. **1893**: 170. 1893; Syll. Fung. **11**: 629. 1895.
129. *C. Cruciferarum* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 619. 1892.
130. *C. cruenta* Sacc. Michelia **2**: 149. 1880; Syll. Fung. **4**: 435. 1886; Jour. Myc. **2**: 1. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 56. 1892; B. P. I. Bull. 226: 49. 1912; N. J. Agr. Sta. Bull. 313: 134. 1917.
131. *C. Cucurbitae* Ell. & Ev. Jour. Myc. **4**: 3. 1888; Syll. Fung. **10**: 634. 1892; Jour. Myc. **4**: 28. 1888; Elisha Mitchell Sci. Soc. Jour. **8**: 45. 1892; B. P. I. Bull. 226: 43, 105. 1912.
132. *C. Cydoniae* Ell. & Ev. Jour. Myc. **8**: 72. 1902; Syll. Fung. **18**: 601. 1906.
133. *C. Cypripedii* Ell. & Dearn. Can. Inst. Trans. **6**: 637. 1899; Syll. Fung. **16**: 1073. 1902; Wisc. Acad. Trans. **16**: 758. 1909; *l. c.* **17**: 891. 1914.
134. *C. Daleae* Ell. & Kell. Jour. Myc. **4**: 6. 1888; Syll. Fung. **10**: 622. 1892.
135. *C. Daturae* Peck, N. Y. Mus. Rept. **35**: 140. 1884; Syll. Fung. **4**: 449. 1886; Jour. Myc. **1**: 62. 1885; Wisc. Acad. Trans. **19**: 689. 1919.
136. *C. Davisii* Ell. & Ev. Acad. Phila. Proc. **1891**: 89. 1891; Syll. Fung. **10**: 622. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 60. 1892; Myc. **1**: 268. 1909; Wisc. Acad. Trans. **9**: 166. 1893; *l. c.* **21**: 275. 1924.
137. *C. Decodontis* Tehon & Daniels, Myc. **17**: 246. 1925.
138. *C. Decumariae* Tracy & Earle, Torr. Bot. Club Bull. **26**: 495. 1899; Syll. Fung. **16**: 1067. 1902.
139. *C. Demetrioniana* Wint. Hedw. **23**: 170. 1884; Syll. Fung. **4**: 439. 1886; Jour. Myc. **1**: 34. 1885.
140. *C. Depazeoides* (Desm.) Sacc. Nuovo Giorn. Bot. Ital. **8**: 187. 1876; Am. Nat. **17**: 1166. 1883, as *C. Sambucina* Ell. & Kell.; Ann. Sci. Nat. Bot. III, **11**: 364. 1849, as *Exosporium Depazeoides* Desm.; Syll. Fung. **4**: 469. 1886; Jour. Myc. **1**: 34. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 61. 1892; Wisc. Acad. Trans. **19**: 688. 1919; Ind. Acad. Proc. **1921**: 146. 1922.
141. *C. Desmanthi* Ell. & Kell. Jour. Myc. **3**: 14. 1887; *l. c.* **1**: 2. 1885, as *C. condensata* var. *Desmanthi* Ell. & Kell.; Syll. Fung. **4**: 462. 1886, as *C. condensata* var. *Desmanthi* Ell. & Kell.; *l. c.* **10**: 641. 1892.
142. *C. Desmodii* Ell. & Kell. Torr. Bot. Club Bull. **11**: 121. 1884; Syll. Fung. **4**: 439. 1886; Jour. Myc. **1**: 50. 1885; Hedw. **24**: 204. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 53. 1892.
143. *C. destructiva* Rav. in Ell. & Ev. Jour. Myc. **3**: 13. 1887; Syll. Fung. **10**: 642. 1892.
144. *C. Deutziae* Ell. & Ev. Jour. Myc. **4**: 5. 1888; Syll. Fung. **10**: 642. 1892.
145. *C. Diantherae* Ell. & Kell. Jour. Myc. **1**: 2, 19. 1885; Syll. Fung. **4**: 448. 1886; B. P. I. Bull. 226: 104. 1912.
146. *C. didymospora* Ell. & Barth. Erythea **4**: 28. 1896; Syll. Fung. **14**: 1100. 1899.

147. *C. Diervillae* Ell. & Ev. Univ. Maine Studies 3: 22. 1902; Syll. Fung. **18**: 605. 1906.
148. *C. diffusa* Ell. & Ev. Jour. Myc. **4**: 3. 1888; Syll. Fung. **10**: 635. 1892; Wisc. Acad. Trans. **21**: 278. 1924.
149. *C. Diodiae* Cooke, Grev. **7**: 34. 1878; Syll. Fung. **4**: 441. 1886; Michelia **2**: 148. 1880; Jour. Myc. **1**: 35. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 44. 1892; N. J. Agr. Sta. Bull. 313: 134. 1917.
150. *C. Diodiae-virginianae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 58. 1892; Syll. Fung. **10**: 645. 1892.
151. *C. Dioscoreae* Ell. & Mart. Am. Nat. **16**: 1003. 1882; Syll. Fung. **4**: 479. 1886; Jour. Myc. **1**: 54. 1885.
152. *C. Diospyri* Thuem. Myc. Univ. 1273. 1879[1]; Syll. Fung. **4**: 467. 1886; Grev. **12**: 31. 1883; Jour. Myc. **1**: 51. 1885.
153. *C. Diospyri* Thuem. var. *ferruginosa* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 63. 1892.
154. *C. dispersa* Ell. & Ev. Jour. Myc. **4**: 115. 1888; Syll. Fung. **10**: 652. 1892.
155. *C. ditissima* Ell. & Ev. Acad. Phila. Proc. **1893**: 171. 1893; Syll. Fung. **11**: 628. 1895.
156. *C. Dolichi* Ell. & Ev. Jour. Myc. **5**: 71. 1889; Syll. Fung. **10**: 622. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 62. 1892; N. J. Agr. Sta. Bull. 313: 134. 1917.
157. *C. dubia* (Riess) Wint. Hedw. **22**: 10. 1883; *l. c.* **1**: *t.4*, *f. 9.* 1854, as *Ramularia dubia* Riess, not Speg.; Syll. Fung. **4**: 456. 1886; Beitr. Myk. 92. 1863, as *C. Chenopodii* Fres.; Michelia **2**: 364. 1881; Jour. Myc. **1**: 19. 1885; N. J. Agr. Sta. Bull. 313: 134. 1917; Wisc. Acad. Trans. **17**: 890. 1914.
158. *C. Dulcamarae* (Peck) Ell. Jour. Myc. **1**: 55. 1885; N. Y. Mus. Rept. **33**: 30. 1880, as *Ramularia Dulcamarae* Peck; Syll. Fung. **4**: 449. 1886.
159. *C. duplicata* Ell. & Ev. Jour. Myc. **5**: 70. 1889; Syll. Fung. **10**: 648. 1892.
160. *C. Echinochloae* Davis, Wisc. Acad. Trans. **18**: 106. 1915.
161. *C. Echinocystis* Ell. & Mart. Am. Nat. **16**: 1003. 1882; Syll. Fung. **4**: 452. 1886; Jour. Myc. **1**: 40. 1885; Wisc. Acad. Trans. **15**: 268. 1915; Myc. **16**: 138. 1924.
162. *C. effusa* (Berk. & Curt.) Ell. Jour. Myc. **1**: 53. 1885; Grev. **3**: 106. 1875, as *Cladosporium effusum* Berk. & Curt.; Syll. Fung. **4**: 447. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 62. 1892.
163. *C. Elaeagni* Heald & Wolf, Myc. **3**: 16. 1911; B. P. I. Bull. 226: 75. 1912.
164. *C. elaeochroma* Sacc. Nuovo Giorn. Bot. Ital. **23**: 220. 1916.
165. *C. Elephantopodis* Ell. & Ev. Jour. Myc. **3**: 15. 1887; Syll. Fung. **10**: 626. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 55. 1892; Iowa Acad. Proc. **7**: 163. 1899.
166. *C. Ellisii* Sacc. & Syd. Syll. Fung. **14**: 1103. 1899; Erythea **5**: 5. 1897, as *C. Hyptidis* Ell. & Ev., not Speg.
167. *C. elongata* Peck, N. Y. Mus. Rept. **33**: 29. 1880; Syll. Fung. **4**: 442. 1886; Syll. Fung. **10**: 629. 1892; Jour. Myc. **1**: 38. 1885; *l. c.* **8**: 121. 1902.

[1] There is no indication in the copy of 'Mycotheca Universalis' at the Missouri Botanical Garden that the present label designating this species as *Cercospora* is an emended label substituted for one designating it as *Helminthosporium*, as would be inferred from 'Sylloge Fungorum' and 'Grevillea.'

168. *C. Epigaeae* Ell. & Dearn. Can. Inst. Trans. **6**: 637. 1899; Syll. Fung. **16**: 1071. 1902.
169. *C. Epigaeina*[1] Davis, Wisc. Acad. Trans. **16**: 758. 1909; Syll. Fung. **22**: 1425. 1913.
170. *C. Epilobii* Schn. Michelia **2**: 642. 1882; Syll. Fung. **4**: 453. 1886; Jour. Myc. **1**: 51. 1885.
171. *C. Erechthitis* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 66. 1892; Syll. Fung. **10**: 629. 1892.
172. *C. Eriogoni* Ell. & Ev. Erythea **5**: 6. 1897; Syll. Fung. **14**: 1105. 1899.
173. *C. Erysimi* Davis, Wisc. Acad. Trans. **18**: 267. 1915.
174. *C. Erythrinae* Ell. & Ev. Jour. Myc. **3**: 18. 1887; Syll. Fung. **10**: 640. 1892.
175. *C. erythrinicola* Tharp, Myc. **9**: 109. 1917.
176. *C. erythrogena* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 65. 1892; Syll. Fung. **10**: 644. 1892.
177. *C. Euonymi* Ell. Am. Nat. **16**: 810. 1882; Syll. Fung. **4**: 466. 1886; Jour. Myc. **1**: 19. 1885; Wisc. Acad. Trans. **21**: 262. 1924.
178. *C. Eupatorii* Peck, N. Y. Mus. Rept. **33**: 29. 1880; Syll. Fung. **4**: 444. 1886; Jour. Myc. **1**: 35. 1885; Iowa Acad. Proc. **7**: 163. 1899.
179. *C. Euphorbiae* Kell. & Sw. Jour. Myc. **5**: 76. 1889, not *C. Euphorbiae* Pat. Soc. Myc. Fr. Bull. **9**: 160. 1893.
180. *C. euphorbiaecola* Atk. Cornell Univ. Bull. **3**[1]: 41. 1897; Syll. Fung. **14**: 1104. 1899.
181. *C. euphorbiaecola* Atk. var. *tragiae* Tharp, Myc. **9**: 109. 1917.
182. *C. Eustomae* Peck, N. Y. Mus. Bull. 157: 45, 107. 1912.
183. *C. exotica* Ell. & Ev. Acad. Phila. Proc. **1893**: 463. 1893; Syll. Fung. **11**: 625. 1895.
184. *C. ferruginea* Fckl. Beitr. Myk. 93. 1863; Syll. Fung. **4**: 444. 1886; Symb. Myc. 354. 1869–70; Jour. Myc. **2**: 1. 1886; *l. c.* **5**: 143. 1889.
185. *C. Fici* Heald & Wolf, Myc. **3**: 16. 1911; B. P. I. Bull. 226: 26. 1912.
186. *C. Ficina* Tharp, Myc. **9**: 109. 1917.
187. *C. filispora* Peck, Jour. Myc. **1**: 36. 1885; Syll. Fung. **4**: 436. 1886.
188. *C. fingens* Davis, Wisc. Acad. Trans. **18**: 92. 1915.
189. *C. flagellaris* Ell. & Mart. Am. Nat. **16**: 1003. 1882; Syll. Fung. **4**: 453. 1886; Jour. Myc. **1**: 18. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 46. 1892; B. P. I. Bull. 226: 99, 101. 1912.
190. *C. flagellifera* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 51. 1892; Syll. Fung. **10**: 622. 1892; Wisc. Acad. Trans. **20**: 429. 1922; *l. c.* **21**: 258. 1924.
191. *C. flagelliformis* Ell. & Halst. N. J. Agr. Sta. Rept. **11**: 355. 1890, nomen nudum; U. S. D. A. Bull. 1366. 1926.
192. *C. flexuosa* Tracy & Earle, Torr. Bot. Club Bull. **22**: 178. 1895; Syll. Fung. **14**: 1101. 1899.
193. *C. floricola* Heald & Wolf, Myc. **3**: 17. 1911; B. P. I. Bull. 226: 106. 1912.
194. *C. Fraxinea* Ell. & Ev. Jour. Myc. **4**: 4. 1888; Syll. Fung. **10**: 646. 1892.
195. *C. Fraxinites* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 647. 1892; B. P. I. Bull. 226: 57. 1912.
196. *C. fuliginosa* Ell. & Kell. Jour. Myc. **3**: 103. 1887, as *C. fuligniosa;* Syll. Fung. **10**: 648. 1892; B. P. I. Bull. 226: 30. 1912.

[1] J. J. Davis in Wisc. Acad. Trans. **21**: 275. 1924, says: " . . . evidently not distinct from *C. Epigaeae* Ell. & Dearn. which is the older name."

197. *C. fulvella* Heald & Wolf, Myc. **3**: 17. 1911; B. P. I. Bull. 226: 93. 1912.
198. *C. fuscovirens* Sacc. Michelia **2**: 149. 1880; Syll. Fung. **4**: 452. 1886; Jour. Myc. **1**: 53. 1885; *l. c.* **5**: 72. 1889; Elisha Mitchell Sci. Soc. Jour. **8**: 63. 1892.
199. *C. fusimaculans* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 50. 1892; Syll. Fung. **10**: 655. 1892; Myc. **14**: 198. 1922.
200. *C. Galactiae* Ell. & Ev. Torr. Bot. Club Bull. **22**: 438. 1895; Syll. Fung. **14**: 1100. 1899.
201. *C. Galii* Ell. & Holw. Jour. Myc. **1**: 5. 1885; Syll. Fung. **4**: 441. 1886; Jour. Myc. **1**: 39. 1885; *l. c.* **3**: 16. 1887; Elisha Mitchell Sci. Soc. Jour. **8**: 53. 1892; Wisc. Acad. Trans. **17**: 894. 1914; *l. c.* **20**: 405. 1922; *l. c.* **21**. 289. 1924.
202. *C. Garryae* Harkn. Calif. Acad. Bull. **1**: 38. 1884; Syll. Fung. **4**: 474. 1886; Jour. Myc. **1**: 39. 1885.
203. *C. Gaultheriae* Ell. & Ev. Jour. Myc. **2**: 2. 1886; Syll. Fung. **4**: 472. 1886.
204. *C. Gaurae* Kell. & Sw. Jour. Myc. **5**: 75. 1889; Syll. Fung. **10**: 625. 1892.
205. *C. Gayophyti* Ell. & Ev. Torr. Bot. Club Bull. **24**: 474. 1897; Syll. Fung. **14**: 1100. 1899.
206. *C. Gentianae* Peck, N. Y. Mus. Rept. **41**: 80. 1888; Syll. Fung. **10**: 634. 1892.
207. *C. gentianicola* Ell. & Ev. Jour. Myc. **4**: 2. 1888; Syll. Fung. **10**: 633. 1892; Wisc. Acad. Trans. **19**: 688. 1919.
208. *C. Geranii* Kell. & Sw. Jour. Myc. **5**: 74. 1889; Syll. Fung. **10**: 621. 1892; Wisc. Acad. Trans. **11**: 171. 1897; *l. c.* **17**: 892. 1914.
209. *C. Gerardiae* Ell. & Dearn. Can. Rec. Sci. **5**: 271. 1893; Syll. Fung. **11**: 628. 1895; Wisc. Acad. Trans. **14**: 96. 1903; *l. c.* **17**: 894. 1914.
210. *C. glandulosa* Ell. & Kell. Jour. Myc. **1**: 3. 1885; Syll. Fung. **4**: 467. 1886; Jour. Myc. **4**: 28. 1888; B. P. I. Bull. 226: 79. 1912.
211. *C. glomerata* Harkn. Calif. Acad. Bull. **3**: 164. 1885; Syll. Fung. **4**: 472. 1886; Jour. Myc. **1**: 106. 1885.
212. *C. glotidiicola* Tracy & Earle, Torr. Bot. Club Bull. **23**: 206. 1896; Syll. Fung. **14**: 1100. 1899.
213. *C. Gnaphaliacea* Cooke, N. Y. Acad. Ann. **1**: 182. 1878; Syll. Fung. **4**: 444. 1886; Linn. Soc. Bot. Jour. **17**: 142. 1880; Jour. Myc. **2**: 1. 1886; Torr. Bot. Club Bull. **25**: 366. 1898; Wisc. Acad. Trans. **14**: 96. 1903; *l. c.* **17**: 894. 1914.
214. *C. Gnaphalii* Harkn. Calif. Acad. Bull. **1**: 38. 1884; Syll. Fung. **4**: 444. 1886; Jour. Myc. **1**: 49. 1885.
215. *C. Gossypina* Cooke, Grev. **12**: 31. 1883; Syll. Fung. **4**: 441. 1886; Jour. Myc. **1**: 49. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 66. 1892; B. P. I. Bull. 226: 55. 1912.
216. *C. graminicola* Tracy & Earle, Torr. Bot. Club Bull. **22**: 179. 1895; Syll. Fung. **14**: 1106. 1899.
217. *C. granuliformis* Ell. & Holw. Jour. Myc. **1**: 6. 1885; Syll. Fung. **4**: 434. 1886; Jour. Myc. **1**: 40. 1885; N. J. Agr. Sta. Bull. 313: 136. 1917; Ind. Acad. Proc. **1921**: 147. 1922; Wisc. Acad. Trans. **21**: 294. 1924.
218. *C. Gratiolae* Ell. & Ev. Jour. Myc. **8**: 71. 1902; Syll. Fung. **18**: 604. 1906.
219. *C. Grindeliae* Ell. & Ev. Acad. Phila. Proc. **1895**: 439. 1896; Syll. Fung. **14**: 1101. 1899; Wisc. Acad. Trans. **18**: 269. 1915.

220. *C. grisea* Cooke & Ell. Grev. **5**: 49. 1876; Syll. Fung. **4**: 434. 1886, as *C. minuta* Cooke & Ell., probably an error for *C. grisea* Cooke & Ell.; Grev. **6**: 89. 1878; Jour. Myc. **1**: 53. 1885.
221. *C. grisella* Peck, N. Y. Mus. Rept. **33**: 29. 1880; Syll. Fung. **4**: 443. 1886; Jour. Myc. **1**: 62. 1885.
222. *C. guttulata* Ell. & Kell. Jour. Myc. **9**: 105. 1903; Syll. Fung. **18**: 608. 1906.
223. *C. Gymnocladi* Ell. & Kell. Torr. Bot. Club Bull. **11**: 121. 1884; Syll. Fung. **4**: 464. 1886; Jour. Myc. **1**: 23. 1885.
224. *C. Halstedii* Ell. & Ev. Acad. Phila. Proc. **1891**: 90. 1891; Syll. Fung. **10**: 651. 1892.
225. *C. Hanseni* Ell. & Ev. Erythea **1**: 147. 1893; Syll. Fung. **11**: 629. 1895.
226. *C. Helenii* Tharp, Myc. **9**: 110. 1917.
227. *C. Helianthi* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 628. 1892; Jour. Myc. **4**: 6, 28. 1888; *l. c.* **10**: 56. 1904; Wisc. Acad. Trans. **20**: 422. 1922.
228. *C. Heliotropii* Ell. & Ev. Jour. Myc. **4**: 5. 1888; Syll. Fung. **10**: 630. 1892.
229. *C. helvola* Sacc. Michelia **2**: 556. 1882; Syll. Fung. **4**: 437. 1886; Jour. Myc. **4**: 7. 1888.
230. *C. helvola* Sacc. var. *Medicaginis*[1] Chester, according to Jour. Myc. **6**: 81. 1890.
231. *C. Hemerocallis* Tehon, Myc. **16**: 139. 1924.
232. *C. Herrerana* Farneti, Bot. Univ. Pavia Atti, II, **9**: 37. 1904; Syll. Fung. **18**: 606. 1906.
233. *C. Heteromeles* Harkn. Calif. Acad. Bull. **1**: 38. 1884; Syll. Fung. **4**: 461. 1886; Jour. Myc. **1**: 24. 1885.
234. *C. heterospora* Ell. & Ev. Torr. Bot. Club Bull. **25**: 512. 1898; Syll. Fung. **16**: 1072. 1902.
235. *C. Heucherae* Ell. & Mart. Am. Nat. **18**: 189. 1884; Syll. Fung. **4**: 453. 1886; Jour. Myc. **1**: 34. 1885.
236. *C. Hibisci* Tracy & Earle, Torr. Bot. Club Bull. **22**: 179. 1895; Syll. Fung. **14**: 1099. 1899.
237. *C. Hibiscina* Ell. & Ev. Acad. Phila. Proc. **1895**: 438. 1896; Syll. Fung. **14**: 1099. 1899.
238. *C. Hieracii* Ell. & Ev. Jour. Myc. **8**: 70. 1902; Syll. Fung. **18**: 607. 1906.
239. *C. Houstoniae* Ell. & Ev. Acad. Phila. Proc. **1891**: 89. 1891; Syll. Fung. **10**: 634. 1892.
240. *C. Hydrangeae* Ell. & Ev. in Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 52. 1892; Syll. Fung. **18**: 602. 1906; Jour. Myc. **8**: 71. 1902.
241. *C. Hydrangeana* Tharp, Myc. **9**: 110. 1917.
242. *C. Hydrocotyles* Ell. & Ev. Jour. Myc. **3**: 16. 1887; Syll. Fung. **10**: 624. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 55. 1892; Iowa Acad. Proc. **7**: 164. 1899; B. P. I. Bull. 226: 96. 1912.
243. *C. Hydropiperis* (Thuem.) Speg. Soc. Cien. Argent. Anal. **1**: 191. 1867;[2] Myc. Univ. 1087, as *Helminthosporium Hydropiperis* Thuem.; Syll. Fung. **4**: 455. 1886; Hedw. **17**: 39. 1878, as *C. polygonorum* Cooke; Jour. Myc. **1**: 52. 1885, as *C. polygonorum* Cooke; *l. c.* **8**: 58. 1902; Myc. **8**: 43. 1916.

[1] Delaware Agr. Sta. Rept. **2**: 94–97. 1890, which is given as the original citation, does not appear to contain the description.

[2] It has been impossible to verify this citation.

244. *C. Hyperici* Tehon & Daniels, Myc. **19**: 127. 1927.
245. *C. Ichthyomethiae* Dearn. & Barth. Myc. **16**: 175. 1924.
246. *C. ilicicola* Lieneman, nom. nov.
(*C. Ilicis* Maublanc, Algunos fungos do Brazil [other data unknown], not *C. Ilicis* Ell. Torr. Bot. Club Bull. **8**: 65. 1881; Myc. **9**: 110. 1917.)
247. *C. Ilicis* Ell. Torr. Bot. Club Bull. **8**: 65. 1881; Syll. Fung. **4**: 467. 1886; Jour. Myc. **1**: 24. 1885; N. J. Agr. Sta. Bull. 313: 136. 1917.
248. *C. illinoensis* Barth. Fungi Columb. 2611. 1908; Syll. Fung. **22**: 1428. 1913.
249. *C. incarnata* Ell. & Ev. Torr. Bot. Club Bull. **24**: 474. 1897; Syll. Fung. **14**: 1103. 1899.
250. *C. infuscans* Ell. & Ev. Acad. Phila. Proc. **1891**: 90. 1891; Syll. Fung. **10**: 639. 1892.
251. *C. inquinans* Cooke, Grev. **7**: 12. 1878; Syll. Fung. **4**: 465. 1886; Jour. Myc. **1**: 36. 1885.
252. *C. Ipomoeae* Wint. Hedw. **26**: 34. 1887; Syll. Fung. **10**: 633. 1892; Jour. Myc. **4**: 7. 1888.
253. *C. Isanthi* Ell. & Kell. Torr. Bot. Club Bull. **11**: 115. 1884; Syll. Fung. **4**: 447. 1886; Jour. Myc. **1**: 21. 1885.
254. *C. Jatrophae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 64. 1892; Syll. Fung. **10**: 650. 1892.
255. *C. Juglandis* Kell. & Sw. Jour. Myc. **5**: 77. 1889; Syll. Fung. **10**: 651. 1892.
256. *C. Jussieuae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 50. 1892; Syll. Fung. **10**: 625. 1892.
257. *C. Kaki* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 648. 1892; B. P. I. Bull. 226: 31. 1912.
258. *C. Kalmiae* Ell. & Ev. Acad. Phila. Proc. **1891**: 88. 1891; Syll. Fung. **10**: 650. 1892.
259. *C. kansensis* Syd. Ann. Myc. **5**: 340. 1907; Syll. Fung. **22**: 1426. 1913.
260. *C. Kellermani* Bubák, Jour. Myc. **9**: 3. 1903; Syll. Fung. **18**: 597. 1906; Jour. Myc. **9**: 24. 1903.
261. *C. Langloisii* Sacc. Syll. Fung. **10**: 647. 1892; Jour. Myc. **3**: 21. 1887, as *C. pallida* Ell. & Ev., not Berk. & Curt.
262. *C. lanuginosa* Heald & Wolf, Myc. **3**: 17. 1911; B. P. I. Bull. 226: 60. 1912.
263. *C. latens* Ell. & Ev. Jour. Myc. **4**: 3. 1888; Syll. Fung. **10**: 641. 1892.
264. *C. lateritia* Ell. & Halst. Jour. Myc. **4**: 7. 1888; Syll. Fung. **10**: 646. 1892.
265. *C. Lathyri* Dearn. & House, N. Y. Mus. Bull. 188: 30. 1916.
266. *C. Lathyrina* Ell. & Ev. Acad. Phila. Proc. **1891**: 91. 1891; Syll. Fung. **10**: 621. 1892.
267. *C. Leonotidis* Cooke, Grev. **8**: 72. 1879; Syll. Fung. **4**: 470. 1886; Syll. Fung. **10**: 631. 1892; Jour. Myc. **3**: 18. 1887.
268. *C. Lepidii* Peck, N. Y. Mus. Rept. **35**: 140. 1884; Syll. Fung. **4**: 432. 1886; Jour. Myc. **1**: 62. 1885.
269. *C. leptosperma*[1] Peck, N. Y. Mus. Rept. **30**: 55. 1878; Syll. Fung. **4**: 442. 1886; Jour. Myc. **1**: 38. 1885.

[1] Davis in Wisc. Acad. Trans. **19**: 706. 1919, says "Instead of *Cercospora leptosperma* Pk. or *Cylindrosporium leptospermum* Pk., I am now using *Cercosporella leptosperma* Pk." and in *l. c.* **20**: 401. 1922, he gives "*Septoriopsis Leptosperma* (Pk.) n. comb."

270. *C. Lespedezae* Ell. & Dearn. Can. Inst. Proc. **1**: 91. 1897; Syll. Fung. **14**: 1100. 1899.
271. *C. leucosticta* Ell. & Ev. Jour. Myc. **4**: 53. 1888; Syll. Fung. **10**: 640. 1892.
272. *C. Ligustri* Roum. Rev. Myc. **5**: 177. 1883; Syll. Fung. **4**: 471. 1886; B. P. I. Bull. 226: 77. 1912.
273. *C. lilacis* (Desm.) Sacc. Michelia **2**: 128. 1880; Ann. Sci. Nat. Bot. III, **11**: 364. 1849, as *Exosporium lilacis* Desm.; Syll. Fung. **4**: 471. 1886; U. S. D.A. Bull. 1366. 1926.
274. *C. Lini* Ell. & Ev. Jour. Myc. **3**: 16. 1887; Syll. Fung. **10**: 620. 1892.
275. *C. Lippiae* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 632. 1892; Wisc. Acad. Trans. **17**: 893. 1914.
276. *C. Liriodendri* Ell. & Harkn. Torr. Bot. Club Bull. **8**: 27. 1881; Syll. Fung. **4**: 459. 1886; Jour. Myc. **1**: 37. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 67. 1892.
277. *C. Lobeliae* Kell. & Sw. Jour. Myc. **5**: 75. 1889; Syll. Fung. **10**: 631. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 47. 1892.
278. *C. longispora*[1] Peck, N. Y. Mus. Rept. **35**: 141. 1884; Syll. Fung. **4**: 436. 1886; Jour. Myc. **1**: 63. 1885; Wisc. Acad. Trans. **19**: 702. 1919.
279. *C. Ludwigiae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 58. 1892; Syll. Fung. **10**: 625. 1892.
280. *C. lumbricoides* Turconi & Maffei, Bot. Univ. Pavia Atti, II, **12**: 330. 1915; Syll. Fung. **22**: 1423. 1913.
281. *C. Lupini* Cooke, Hedw. **17**: 39. 1878; Syll. Fung. **4**: 436. 1886; Jour. Myc. **1**: 55. 1885.
282. *C. lupinicola* Lieneman, nom. nov.
    (*C. texensis* Tharp, Myc. **9**: 115. 1917, not *C. texensis* Ell. & Gall. Jour. Myc. **4**: 116. 1888.)
283. *C. Lycii* Ell. & Halst. Jour. Myc. **4**: 7. 1888; Syll. Fung. **10**: 649. 1892.
284. *C. Lycopi* Ell. & Ev. Jour. Myc. **3**: 15. 1887; Syll. Fung. **10**: 630. 1892.
285. *C. Lysimachiae* Ell. & Halst. Jour. Myc. **6**: 34. 1890; Syll. Fung. **10**: 631. 1892.
286. *C. Lythracearum* Heald & Wolf, Myc. **3**: 18. 1911; B. P. I. Bull. 226: 64, 76. 1912.
287. *C. Lythri* (Westd.) Niessl. Hedw. **15**: 1. 1876; Syll. Fung. **4**: 452. 1886; Acad. Roy. Sci. Belgique Bull. **21**^{2}: 240. 1854, as *Cladosporium Lythri* Westd.; Wisc. Acad. Trans. **14**: 96. 1903; *l. c.* **17**: 893. 1914.
288. *C. MacClatchieana*[2] Sacc. & Syd. Syll. Fung. **14**: 1106. 1899; Erythea **2**: 26. 1894, as *C. fuliginosa* Ell. & Ev., not *C. fuliginosa* Ell. & Kell.; Syll. Fung. **11**: 626. 1895, as *C. fuliginosa* Ell. & Ev., not *C. fuliginosa* Ell. & Kell.

[1] Davis in Wisc. Acad. Trans. **20**: 401. 1922, has cited this fungus as "*Septoriopsis Longispora* (Pk.) n. comb."

[2] J. J. Davis, in Wisc. Acad. Trans. **18**: 86. 1915, says that *C. Ceanothi* Kell. & Sw. is present earlier in life and *C. fuliginosa* Ell. & Ev. later in life of plant. "It is probable . . . that the description of *C. Ceanothi* Kell. & Swingle and *C. fuliginosa* Ell. & Evht. were drawn from different states of the same fungus. The former is the prior name and the latter is antedated by *C. fuliginosa* Ell. & Kell. on *Diospyros* (1887) for which reason *C. MacClatchieana* Sacc. & Syd. was substituted."

289. *C. Maclurae* Ell. & Ev. Jour. Myc. **8**: 72. 1902; Syll. Fung. **18**: 610. 1906.
290. *C. macrochaeta* Ell. & Ev. Torr. Bot. Club Bull. **24**: 473. 1897; Syll. Fung. **14**: 1105. 1899.
291. *C. macroguttata* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 64. 1892; Syll. Fung. **10**: 628. 1892.
292. *C. macromaculans* Heald & Wolf, Myc. **3**: 18. 1911; B. P. I. Bull. 226: 70. 1912.
293. *C. Magnoliae* Ell. & Harkn. Torr. Bot. Club Bull. **8**: 27. 1881; Syll. Fung. **4**: 459. 1886; Jour. Myc. **1**: 35. 1885; N. J. Agr. Sta. Bull. 313: 136. 1917.
294. *C. Majanthemi* Fckl. Symb. Myc. 353. 1869–70; Syll. Fung. **4**: 476. 1886; *l. c.* **10**: 654. 1892; Jour. Myc. **9**: 111. 1903; Myc. **18**: 179. 1926.
295. *C. Malachrae*[1] Heald & Wolf, Myc. **3**: 19. 1911; B. P. I. Bull. 226: 97. 1912.
296. *C. Mali* Ell. & Ev. Jour. Myc. **4**: 116. 1888; Syll. Fung. **10**: 643. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 55. 1892; B. P. I. Bull. 226: 24. 1912.
297. *C. Malloti* Ell. & Ev. Jour. Myc. **4**: 114. 1888; Syll. Fung. **10**: 650. 1892.
298. *C. maritima* Tracy & Earle, Torr. Bot. Club Bull. **22**: 179. 1895; Syll. Fung. **14**: 1104. 1899.
299. *C. Marrubii* Tharp, Myc. **9**: 111. 1917.
300. *C. Medicaginis* Ell. & Ev. Acad. Phila. Proc. **1891**: 91. 1891; Syll. Fung. **10**: 622. 1892; B. P. I. Bull. 226: 48. 1912; Phytopath. **6**: 301. 1916; N. J. Agr. Sta. Bull. 313: 138. 1917; Wisc. Acad. Trans. **20**: 429. 1922.
301. *C. megalopotamica* Speg. Anal. Soc. Sci. Argent. **13**: 29. 1882; Syll. Fung. **4**: 443. 1886; Wisc. Acad. Trans. **16**: 758. 1909; *l. c.* **17**: 895. 1914; *l. c.* **18**: 256. 1915.
302. *C. melaleuca* Ell. & Ev. Torr. Bot. Club Bull. **27**: 56. 1900; Syll. Fung. **16**: 1068. 1902.
303. *C. melanochaeta* Ell. & Ev. Acad. Phila. Proc. **1894**: 380. 1894; Syll. Fung. **11**: 627. 1895.
304. *C. Meliae* Ell. & Ev. Jour. Myc. **3**: 16. 1887; Syll. Fung. **10**: 639. 1892.
305. *C. Menispermi* Ell. & Holw. Jour. Myc. **4**: 6. 1888; Syll. Fung. **10**: 618. 1892; B. P. I. Bull. 226: 92. 1912; Myc. **16**: 138. 1924.
306. *C. menthicola* Tehon & Daniels, Myc. **17**: 247. 1925.
307. *C. Merrowii* Ell. & Ev. Acad. Phila. Proc. **1894**: 380. 1894; Syll. Fung. **11**: 625. 1895.
308. *C. microsora* Sacc. Michelia **2**: 128. 1880; Bot. Gaz. **6**: 277. 1881, as *C. Tiliae* Peck; Jour. Myc. **1**: 35. 1885, as *C. Tiliae* Peck; Syll. Fung. **4**: 459. 1886; N. J. Agr. Sta. Bull. 313: 138. 1917.
309. *C. microstigma* Sacc. Ann. Myc. **10**: 315. 1912; Syll. Fung. **22**: 1431. 1913.
310. *C. Mikaniae* Ell. & Ev. Acad. Phila. Proc. **1891**: 90. 1891; Syll. Fung. **10**: 629. 1892.
311. *C. Mimuli* Ell. & Ev. Jour. Myc. **3**: 18. 1887; Syll. Fung. **10**: 631. 1892.

[1] Seaver & Chardon (Sci. Surv. Porto Rico 8^1: 95. 1926) refer *C. Malachrae* Young (Myc. **8**: 45. 1916) as a synonym of the species. The descriptions are very much alike, but Chardon does not state that he studied authentic material of Young's species. In case they are different, the latter must be renamed.

312. *C. minima* Tracy & Earle, Torr. Bot. Club Bull. **23**: 206. 1896; Syll. Fung. **14**: 1100. 1899; B. P. I. Bull. 226: 30. 1912.

313. *C. Mirabilis* Tharp, Myc. **9**: 111. 1917.

314. *C. Modiolae* Tharp, Myc. **9**: 111. 1917.

315. *C. Molluginis* Halst. Torr. Bot. Club Bull. **20**: 251. 1893.

316. *C. molluginicola* Lieneman, nom. nov.
(*C. Molluginis* Davis, Wisc. Acad. Trans. **21**: 285. 1924, not *C. Molluginis* Halst. Torr. Bot. Club Bull. **20**: 251. 1893.)

317. *C. monoica* Ell. & Holw. Jour. Myc. **1**: 6, 49. 1885; Syll. Fung. **4**: 438. 1886.

318. *C. montana* (Speg.) Sacc. Dec. Myc. 104. 1879, as *Ramularia montana* Speg.; Syll. Fung. **4**: 453. 1886; Nuovo Giorn. Bot. Ital. **23**: 220. 1916; Myc. **10**: 263. 1918; Wisc. Acad. Trans. **9**: 167. 1892; *l. c.* **15**: 780. 1907; *l. c.* **16**: 746. 1909.

319. *C. moricola* Cooke, Grev. **12**: 30. 1883; Syll. Fung. **4**: 475. 1886; Jour. Myc. **1**: 34. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 43. 1892; Cornell Univ. Bull. **3**[1]: 41. 1897; B. P. I. Bull. 226: 74. 1912; Wisc. Acad. Trans. **21**: 261. 1924.

320. *C. Morongiae* Tracy & Earle, Torr. Bot. Club Bull. **26**: 495. 1899; Syll. Fung. **16**: 1074. 1902.

321. *C. Muhlenbergiae* Atk. Cornell Univ. Bull. **3**[1]: 46. 1897; Syll. Fung. **14**: 1106. 1899; Wisc. Acad. Trans. **20**: 421. 1922.

322. *C. murina* Ell. & Kell. Torr. Bot. Club Bull. **11**: 122. 1884; Syll. Fung. **4**: 434. 1886; Jour. Myc. **1**: 53. 1885; Ind. Acad. Proc. **1921**: 147. 1921.

323. *C. Myricae* Tracy & Earle, Torr. Bot. Club Bull. **23**: 206. 1896; Syll. Fung. **14**: 1105. 1899.

324. *C. Namae* Dearn. & House, N. Y. Mus. Bull. 179: 34. 1915.

325. *C. Nasturtii* Pass. Hedw. **16**: 124. 1877; Syll. Fung. **4**: 433. 1886; Jour. Myc. **3**: 16. 1887; Wisc. Acad. Trans. **11**: 171. 1897; *l. c.* **19**: 687. 1919; *l. c.* **21**: 294. 1924; B. P. I. Bull. 226: 104. 1912; Ind. Acad. Proc. **1921**: 147. 1922.

326. *C. Negundinis* Ell. & Ev. Acad. Phila. Proc. **1891**: 89. 1891; Syll. Fung. **10**: 638. 1892.

327. *C. Nelumbonis* Tharp, Myc. **9**: 111. 1917.

328. *C. Nepetae* Tehon, Myc. **16**: 140. 1924.

329. *C. Nepheloides* Ell. & Holw. B. P. I. Bull. 226: 87. 1912.

330. *C. neriella* Sacc. Michelia **2**: 294. 1881; Syll. Fung. **4**: 473. 1886; U. S. D. A. Bull. 1366. 1926.

331. *C. Nesacae* Ell. & Ev. Acad. Phila. Proc. **1893**: 170. 1893; Syll. Fung. **11**: 625. 1895.

332. *C. Nicotianae* Ell. & Ev. Acad. Phila. Proc. **1893**: 170. 1893; Syll. Fung. **11**: 628. 1895; B. P. I. Bull. 226: 105. 1912.

333. *C. nigri* Tharp, Myc. **9**: 112. 1917.

334. *C. nigricans* Cooke, Grev. **12**: 30. 1883; Syll. Fung. **4**: 462. 1886; Jour. Myc. **1**: 52. 1885.

335. *C. noveboracensis* Ell. & Ev. Jour. Myc. **3**: 14. 1887; Syll. Fung. **10**: 628. 1892.

336. *C. nubilosa*[1] Ell. & Ev. Jour. Myc. **4**: 115. 1888; Syll. Fung. **10**: 654. 1892; Mo. Bot. Gard. Ann. **14**: 425. 1927.
337. *C. Nymphaeacea* Cooke & Ell. Grev. **6**: 89. 1878; Syll. Fung. **4**: 432. 1886; Jour. Myc. **1**: 22. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 54. 1892; Wisc. Acad. Trans. **14**: 97. 1903; *l. c.* **17**: 891. 1914.
338. *C. Nyssae* Tharp, Myc. **9**: 112. 1917.
339. *C. obesa* Ell. & Ev. Jour. Myc. **4**: 5. 1888; Syll. Fung. **10**: 626. 1892; N. J. Agr. Sta. Bull. 313: 140. 1917.
340. *C. obscura* Heald & Wolf, Myc. **3**: 19. 1911; B. P. I. Bull. 226: 40. 1912.
341. *C. occidentalis* Cooke, Hedw. **17**: 39. 1878; Syll. Fung. **4**: 463. 1886; Jour. Myc. **1**: 50. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 43. 1892; B. P. I. Bull. 226: 101. 1912.
342. *C. oculata* Ell. & Kell. Torr. Bot. Club Bull. **11**: 116. 1884; Syll. Fung. **4**: 443. 1886; Jour. Myc. **1**: 22. 1885.
343. *C. Oenotherae* Ell. & Ev. Acad. Phila. Proc. **1894**: 380. 1894; Syll. Fung. **11**: 625. 1895.
344. *C. Oenotherae-sinuatae* Atk. Cornell Univ. Bull. **3**[1]: 46. 1897; Syll. Fung. **14**: 1099. 1899.
345. *C. olivacea*[2] (Berk. & Rav.) Ell. Jour. Myc. **1**: 52. 1885; Grev. **3**: 102. 1875, as *Helminthosporium olivaceum* Berk. & Rav.; Syll. Fung. **4**: 462. 1886.
346. *C. omphakodes* Ell. & Holw. Jour. Myc. **1**: 5, 23. 1885; Syll. Fung. **4**: 447. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 42. 1892; Torr. Bot. Club Bull. **25**: 366. 1898.
347. *C. Oryzae* Miyake, Tokyo Coll. Agr. Jour. **2**: 263. 1910; Syll. Fung. **22**: 1431. 1913; U. S. D. A. Bull. 1366. 1926.
348. *C. Osmorhizae* Ell. & Ev. Acad. Phila. Proc. **1891**: 89. 1891; Syll. Fung. **10**: 624. 1892; Wisc. Acad. Trans. **20**: 421. 1922.
349. *C. Oxybaphi* Ell. & Halst. Jour. Myc. **4**: 8. 1888; Syll. Fung. **10**: 636. 1892; Wisc. Acad. Trans. **21**: 258. 1924.
350. *C. Oxydendri*[3] Tracy & Earle, Torr. Bot. Club Bull. **26**: 495. 1899; Syll. Fung. **16**: 1067. 1902.
351. *C. pachypus* Ell. & Kell. Jour. Myc. **3**: 104. 1887; Syll. Fung. **10**: 628. 1892; Jour. Myc. **4**: 7, 29. 1888; B. P. I. Bull. 226: 103. 1912.
352. *C. pachyspora* Ell. & Ev. Acad. Phila. Proc. **1891**: 88. 1891; Syll. Fung. **10**: 654. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 45. 1892.
353. *C. Paeoniae* Tehon & Daniels, Myc. **17**: 247. 1925.
354. *C. Pancratii* Ell. & Ev. Jour. Myc. **3**: 15. 1887; Syll. Fung. **10**: 654. 1892.

[1] The original citation gives *Smilax* as host, but from type material in the herbarium of the Missouri Botanical Garden, the host has been determined as *Dioscorea villosa*.—*Cf.* Mo. Bot. Gard. Ann. **14**: 425. 1927.

[2] In Grev. **12**: 30. 1883, Cooke uses the name *C. Berkeleyi* Cooke (*l. c.* and Fungi Am. 777, nomen nudum) to replace *C. olivacea* as above and *Helminthosporium pistillare* Cooke, Fungi Am. 777, nomen nudum. *C. Seymouriana* Wint. Hedw. **22**: 70. 1883, is added by Saccardo (*l. c.*). *C. olivacea* is here treated in this composite sense.

[3] An examination of type material in the herbarium of the Missouri Botanical Garden seems to confirm the similarity between *C. Oxydendri* Tracy & Earle and *C. Oxydendri* Ell. & Ev. Jour. Myc. **8**: 71. 1902; Syll. Fung. **18**: 606. 1906. In this event, the latter should be regarded as a synonym of the former.

355. *C. Panici* Davis, Wisc. Acad. Trans. **19**: 714. 1919.
356. *C. papillosa*[1] Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 52. 1892; Syll. Fung. **10**: 632. 1892.
357. *C. Passaloroides* Wint. Hedw. **22**: 71. 1883; Syll. Fung. **4**: 463. 1886; Jour. Myc. **1**: 50. 1885; Wisc. Acad. Trans. **18**: 106. 1915.
358. *C. Pastinacae* (Sacc.) Peck, N. Y. Mus. Bull. 157: 45, 107. 1912.[2]
359. *C. penicillus* Ell. & Ev. Jour. Myc. **4**: 115. 1888; Syll. Fung. **10**: 652. 1892.
360. *C. Pentstemonis* Ell. & Kell. Torr. Bot. Club Bull. **11**: 121. 1884; Syll. Fung. **4**: 447. 1886; Jour. Myc. **1**: 24. 1885; Ala. Agr. Sta. Bull. 80: 148. 1897; Wisc. Acad. Trans. **9**: 167. 1892; *l. c.* **17**: 894. 1914; *l. c.* **18**: 260. 1915.
361. *C. perfoliata* Ell. & Ev. Jour. Myc. **5**: 71. 1889; Syll. Fung. **10**: 627. 1892; Wisc. Acad. Trans. **9**: 167. 1893; *l. c.* **17**: 894. 1914.
362. *C. perniciosa* Heald & Wolf, Myc. **3**: 19. 1911; B. P. I. Bull. 226: 61. 1912.
363. *C. personata* (Berk. & Curt.) Ell. & Ev. Jour. Myc. **1**: 63. 1885; Grev. **3**: 106. 1875, as *Cladosporium personatum* Berk. & Curt.; Syll. Fung. **4**: 439. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 43. 1892; B. P. I. Bull. 226: 49. 1912; Myc. **9**: 112. 1917; *l. c.* **16**: 138. 1924.
364. *C. personata* (Berk. & Curt.) Ell. & Ev. var. *Cassiae-occidentalis* Sacc. Syll. Fung. **4**: 439. 1886.
365. *C. Phaseolorum* Cooke, Grev. **12**: 30. 1883; Syll. Fung. **4**: 436. 1886; Jour. Myc. **1**: 55. 1885.
366. *C. Phlogina* Peck, N. Y. Mus. Bull. 150: 24. 1911.
367. *C. Phyllitidis* Hume, Torr. Bot. Club Bull. **27**: 577. 1900; Syll. Fung. **16**: 1074. 1902.
368. *C. physalicola* Ell. & Barth. Erythea **4**: 28. 1896; Syll. Fung. **14**: 1102. 1899; B. P. I. Bull. 226: 96. 1912.
369. *C. Physalidis* Ell. Am. Nat. **16**: 810. 1882; Syll. Fung. **4**: 450. 1886; Jour. Myc. **1**: 19. 1885; Wisc. Acad. Trans. **17**: 894. 1914.
370. *C. Piaropi* Tharp, Myc. **9**: 113. 1917.
371. *C. pinnulaecola* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 64. 1892; Syll. Fung. **10**: 640. 1892.
372. *C. Plantaginella* Tehon, Myc. **16**: 139. 1924.
373. *C. Plantaginis* Sacc. Michelia **1**: 267. 1878; Syll. Fung. **4**: 454. 1886; Jour. Myc. **1**: 19. 1885.
374. *C. platanicola* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 652. 1892; Jour. Myc. **9**: 168. 1903.

[1] In Cornell Univ. Bull. **3**[1]: 44. 1897, Atkinson says, "**C. verbenaecola** E. & E. This was described p. 20 Jour. Elisha Mitchell Sci. Soc. VIII, 1892, as a new species, C. papillosa. A later examination of fresh specimens does not seem to show any persistent character which will distinguish it from E. & E's. species."

[2] "*C. Pastinacae* (Sacc.) comb. nov.

"This fungus was originally referred by Mr. Ellis to Cercospora Apii Fres. [Jour. Myc. **1**: 36. 1885], though with some hesitation, as he says he is strongly of the opinion that it will yet prove to be distinct. Prof. Saccardo [Syll. Fung. **4**: 442. 1886] later gave it the name C. Apii Pastinacae Sacc. It appears to us to be a distinct species in its numerous small spots limited by the veinlets of the leaf; in its broader aseptate hyphae and specially in its broader, subcylindric conidia with only 1–3 septa."

375. *C. platyspora*[1] Ell. & Holw. Jour. Myc. **3**: 16. 1887; Syll. Fung. **10**: 625. 1892.
376. *C. Podophylli* Tehon & Daniels, Myc. **19**: 128. 1927.
377. *C. Polygonacea* Ell. & Ev. Jour. Myc. **1**: 24. 1885; Syll. Fung. **4**: 455. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 47. 1892; B. P. I. Bull. 226: 97. 1912.
378. *C. Polytaeniae* Ell. & Kell. Jour. Myc. **3**: 104. 1887; Syll. Fung. **10**: 624. 1892; Wisc. Acad. Trans. **19**: 702. 1919.
379. *C. polytricha* Cooke, Grev. **7**: 35. 1878; Syll. Fung. **4**: 475. 1886; Jour. Myc. **1**: 56. 1885.
380. *C. Pontederiae* Ell. & Dearn. Can. Rec. Sci. **5**: 270. 1893; Syll. Fung. **11**: 629. 1895.
381. *C. populicola* Tharp, Myc. **9**: 113. 1917.
382. *C. Populina* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 651. 1892; Iowa Acad. Proc. **7**: 164. 1899.
383. *C. Prenanthis* Ell. & Kell. Jour. Myc. **3**: 104. 1887; Syll. Fung. **10**: 626. 1892; Tuskegee Exp. Sta. Bull. **4**: 7. 1904.
384. *C. Prosopidis* Heald & Wolf, Myc. **3**: 20. 1911; B. P. I. Bull. 226: 73. 1912.
385. *C. prunicola* Ell. & Ev. Jour. Myc. **3**: 17. 1887; Syll. Fung. **10**: 643. 1892.
386. *C. psedericola* Tehon, Myc. **16**: 139. 1924.
387. *C. Pteleae* Wint. Hedw. **24**: 205. 1885; Syll. Fung. **4**: 465. 1886; Jour. Myc. **1**: 125. 1885.
388. *C. pulcherrimae* Tharp, Myc. **9**: 114. 1917.
389. *C. pulcherrimae minima* Tharp, Myc. **9**: 114. 1917.
390. *C. pulvinula* Cooke & Ell. Grev. **7**: 40. 1878; Syll. Fung. **4**: 467. 1886; Jour. Myc. **1**: 51. 1885.
391. *C. pulvinulata*[2] Sacc. & Wint. Ist. Veneto Atti. **6**^{3}: 728. 1885; Hedw. **24**: 258. 1885, as *C. missouriensis* Wint.; Syll. Fung. **4**: 474. 1886; Jour. Myc. **1**: 106. 1885; B. P. I. Bull. 226: 74. 1912.
392. *C. punctoidea*[3] Ell. & Holw. Wisc. Acad. Trans. **9**: 167. 1893.
393. *C. purpurea* Cooke, Grev. **7**: 34. 1878; Am. Nat. **18**: 189. 1884, as *C. Perseae* Ell. & Mart.; Syll. Fung. **4**: 464. 1886; Jour. Myc. **1**: 34. 1885.
394. *C. Pyri* Farlow, Appalachia **3**: 250. 1884; Syll. Fung. **4**: 461. 1886; Jour. Myc. **1**: 54. 1885; Wisc. Acad. Trans. **17**: 892. 1914.
395. *C. racemosa* Ell. & Mart. Am. Nat. **19**: 76. 1885; Syll. Fung. **4**: 446. 1886; Jour. Myc. **1**: 55. 1885; *l. c.* **3**: 21. 1887.
396. *C. Rafinesquiae* Harkn. Calif. Acad. Bull. **1**: 39. 1884; Syll. Fung. **4**: 445. 1886; Jour. Myc. **1**: 51. 1885.

[1] J. J. Davis in Wisc. Acad. Trans. **21**: 275. 1924 says: "*Cercospora platyspora* Ell. & Holw. is doubtfully distinct from *Cercospora sii* E. & E. and from *Fusicladium depressum* (B. & Br.) Sacc."

[2] As pointed out by Sacc. Syll. Fung. **4**: 474. 1886, *C. pulvinulata* need not be regarded as a homonym because of the existence of *C. pulvinula* Cooke & Ell. Grev. **7**: 40. 1878. *C. missouriensis*, then, becomes a synonym of *C. pulvinulata.*

[3] This is cited as occurring on *Galium trifidum* Ait., but in Wisc. Acad. Trans. **20**: 405. 1922, Davis says: "*Cercospora punctoidea* Ell. & Hol. (in lit.) was recorded in 'A Supplementary List of Parasitic Fungi of Wisconsin,' No. 312 (Trans. Wis. Acad. **9**: 167), but a description was never published presumably because Mr. Ellis concluded it was not distinct."

397. *C. Ranunculi* Ell. & Holw. Jour. Myc. **1**: 5, 50. 1885; Syll. Fung. **4**: 431. 1886; Wisc. Acad. Trans. **20**: 428. 1922.

398. *C. Ratibidae* Ell. & Barth. Jour. Myc. **8**: 177. 1902; Syll. Fung. **18**: 608. 1906; Wisc. Acad. Trans. **21**: 286. 1924.

399. *C. reducta* Syd. Ann. Myc. **1**: 178. 1903; Jour. Myc. **8**: 71. 1902, as *C. sessilis* Ell. & Ev., not Sorok; Syll. Fung. **18**: 610. 1906.

400. *C. regalis* Tharp, Myc. **9**: 114. 1917.

401. *C. repens* Ell. & Ev. Jour. Myc. **3**: 14. 1887; Syll. Fung. **10**: 638. 1892.

402. *C. Resedae* Fckl. Symb. Myc. 353. 1869–70; Syll. Fung. **4**: 435. 1886; Jour. Myc. **1**: 21. 1885; N. J. Agr. Sta. Bull. 313: 140. 1917.

403. *C. Rhamni* Fckl. Symb. Myc. 354. 1869–70; Syll. Fung. **4**: 466. 1886; Jour. Myc. **3**: 16. 1887; Wisc. Acad. Trans. **20**: 416. 1922.

404. *C. Rhapontici* Tehon & Daniels, Myc. **17**: 248. 1925.

405. *C. Rhuina*[1] Cooke & Ell. Grev. **6**: 89. 1878; Syll. Fung. **4**: 467. 1886; Jour. Myc. **1**: 33. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 47. 1892; Iowa Acad. Proc. **7**: 165. 1899; B. P. I. Bull. 226: 78. 1912; N. J. Agr. Sta. Bull. 313: 140. 1917.

406. *C. Rhuina* Cooke & Ell. var. *nigromaculans* Peck, N. Y. Mus. Rept. **42**: 33. 1889.

407. *C. ribicola* Ell. & Ev. Acad. Phila. Proc. **1894**: 379. 1894; Syll. Fung. **11**: 626. 1895; Wisc. Acad. Trans. **15**: 778. 1907.

408. *C. Ribis* Earle, Torr. Bot. Club Bull. **25**: 366. 1898; Syll. Fung. **16**: 1066. 1902.

409. *C. richardiaecola* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 51. 1892; Syll. Fung. **10**: 653. 1892.

410. *C. Ricinella* Sacc. & Berl. Misc. Myc. **2**: 11. 1885; Hedw. **24**: 202. 1885, as *C. albidomaculans* Wint.; Syll. Fung. **4**: 456. 1886; Jour. Myc. **1**: 124. 1885; B. P. I. Bull. 226: 84. 1912.

411. *C. rigospora* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 65. 1892; Syll. Fung. **10**: 635. 1892; Ala. Agr. Sta. Bull. 80: 150. 1897.

412. *C. rosicola* Pass. Myc. Univ. 1086. 1878; Syll. Fung. **4**: 460. 1886; Hedw. **24**: 205. 1885; Jour. Myc. **1**: 35. 1885; *l. c.* **4**: 29. 1888; B. P. I. Bull. 226: 88. 1912; N. J. Agr. Sta. Bull. 313: 140. 1917.

413. *C. rosicola* Pass. var. *undosa* Davis, Wisc. Acad. Trans. **20**: 405. 1922.

414. *C. Rosigena* Tharp, Myc. **9**: 114. 1917.

415. *C. rubella* Cooke, Grev. **7**: 34. 1878; Syll. Fung. **4**: 454. 1886; Jour. Myc. **1**: 22. 1885.

416. *C. Rubi* Sacc. Nuovo Giorn. Bot. Ital. **8**: 188. 1876; Syll. Fung. **4**: 461. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 54. 1892; Cornell Univ. Bull. 3^1: 44. 1897; N. J. Agr. Sta. Bull. 313: 142. 1917; Ind. Acad. Proc. **1921**: 147. 1922.

417. *C. Rubigo* Cooke & Harkn. Grev. **13**: 17. 1884; Syll. Fung. **4**: 461. 1886; Jour. Myc. **1**: 40. 1885; Wisc. Acad. Trans. **17**: 892. 1914; *l. c.* **20**: 429. 1922.

418. *C. rubrotincta* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 643. 1892.

419. *C. Rudbeckiae* Peck, N. Y. Mus. Bull. 131: 19. 1909; Syll. Fung. **22**: 1427. 1918; Wisc. Acad. Trans. **21**: 289. 1924.

[1] According to Jour. Myc. **1**: 33. 1885, *C. copallina* Cooke, Grev. **12**: 31. 1883, and Syll. Fung. **4**: 468. 1886, is a synonym of *C. Rhuina* Cooke & Ell.

420. *C. Sabbatiae* Ell. & Ev. Jour. Myc. **4**: 3. 1888; Syll. Fung. **10**: 634. 1892.
421. *C. Sagittariae* Ell. & Kell. Jour. Myc. **2**: 1. 1886; Syll. Fung. **4**: 479. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 61. 1892; Wisc. Acad. Trans. **14**: 89. 1903; B. P. I. Bull. 226: 90. 1912; Wisc. Acad. Trans. 17: 890. 1914.
422. *C. Salicina* Ell. & Ev. Jour. Myc. **3**: 19. 1887; Syll. Fung. **10**: 651. 1892; B. P. I. Bull. 226: 82. 1912.
423. *C. salviicola* Tharp, Myc. **9**: 115. 1917.
424. *C. Sanguinariae* Peck, N. Y. Mus. Rept. **33**: 29. 1880; Syll. Fung. **4**: 433. 1886; Jour. Myc. **1**: 50. 1885; Wisc. Acad. Trans. **15**: 267. 1915.
425. *C. Saniculae* Davis, Wisc. Acad. Trans. **19**: 687. 1919; *l. c.* **21**: 275. 1924.
426. *C. Sauruři* Ell. & Ev. Jour. Myc. **3**: 14. 1887; Syll. Fung. **10**: 652. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 54. 1892.
427. *C. Scolecotrichoides* Atk. Cornell Univ. Bull. **3**^{1}: 46. 1897; Syll. Fung. **14**: 1106. 1899.
428. *C. Scutellariae* Ell. & Ev. Jour. Myc. **4**: 54. 1888; Syll. Fung. **10**: 630. 1892.
429. *C. Sedi* Ell. & Ev. Jour. Myc. **8**: 72. 1902; Syll. Fung. **18**: 596. 1906.
430. *C. Sedoidis* Ell. & Ev. Jour. Myc. **4**: 4. 1888; Syll. Fung. **10**: 623. 1892.
431. *C. seminalis* Ell. & Ev. Jour. Myc. **4**: 4. 1888; Syll. Fung. **10**: 656. 1892.
432. *C. Senecionis* Ell. & Ev. Acad. Phila. Proc. **1891**: 90. 1891; Syll. Fung. **10**: 629. 1892.
433. *C. septatissima* Tracy & Earle, Torr. Bot. Club Bull. **23**: 206. 1896; Syll. Fung. **14**: 1103. 1899.
434. *C. septorioides* Ell. & Ev. Field Mus. Bot. Ser. Rept. **1**: 94. 1896; Syll. Fung. **14**: 1101. 1899.
435. *C. Sequoiae* Ell. & Ev. Jour. Myc. **3**: 13. 1887; Syll. Fung. **10**: 653. 1892; Wisc. Acad. Trans. **16**: 746. 1909.
436. *C. Sequoiae Juniperi* Ell. & Ev. Jour. Myc. **3**: 14. 1887; Syll. Fung. **10**: 653. 1892.
437. *C. seriata* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 59. 1892; Syll. Fung. **10**: 657. 1892.
438. *C. Serpentariae* Ell. & Ev. Jour. Myc. **3**: 13. 1887; Syll. Fung. **10**: 636. 1892.
439. *C. Setariae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 50. 1892; Syll. Fung. **10**: 655. 1892; Ala. Agr. Sta. Bull. 80: 151. 1897.
440. *C. setariicola* Tehon & Daniels, Myc. **19**: 128. 1927.
441. *C. sidaecola* Ell. & Ev. Jour. Myc. **5**: 72. 1889.
442. *C. Sii* Ell. & Ev. Jour. Myc. **5**: 71. 1889; Syll. Fung. **10**: 624. 1892.
443. *C. Silphii* Ell. & Ev. Jour. Myc. **4**: 3, 29. 1888; Syll. Fung. **10**: 628. 1892; Elisha Mitchell Sci. Soc. Jour. **8**: 60. 1892.
444. *C. Silphii* Ell. & Ev. var. *laciniati* Tehon & Daniels, Myc. **19**: 128. 1927.
445. *C. simulans* Ell. & Kell. Jour. Myc. **8**: 14. 1902; Syll. Fung. **18**: 599. 1906.
446. *C. simulata* Ell. & Ev. Jour. Myc. **1**: 64. 1885; Syll. Fung. **4**: 463. 1886.
447. *C. Smilacina*[1] Sacc. Michelia **2**: 364. 1881; N. Y. Mus. Rept. **33**: 29. 1880, as *C. Smilacis* Peck; Syll. Fung. **4**: 476. 1886; B. P. I. Bull. 226: 102. 1912.

[1] *C. Petersii* (Berk. & Curt.) Atk. is made a synonym in Mo. Bot. Gard. Ann. **14**: 429. 1927. It was described in Elisha Mitchell Sci. Soc. Jour. **8**: 57. 1892, Grev. **3**: 102. 1875, and Syll. Fung. **4**: 421. 1886, as *Helminthosporium Petersii* Berk. & Curt.

448. *C. Smilacinae* Ell. & Ev. Torr. Bot. Club Bull. **27**: 577. 1900; Syll. Fung. **16**: 1073. 1902.
449. *C. Smilacis* Thuem. Hedw. **19**: 35. 1880; Syll. Fung. **4**: 476. 1886; Torr. Bot. Club Bull. **22**: 179. 1895, as *C. mississippiensis* Tracy & Earle; Syll. Fung. **14**: 1105. 1899, as *C. mississippiensis* Tracy & Earle; Jour. Myc. **1**: 33. 1885; Mo. Bot. Gard. Ann. **14**: 428. 1917.
450. *C. solanicola* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 53. 1892; Syll. Fung. **10**: 635. 1892.
451. *C. sordida* Sacc. Michelia **2**: 149. 1880; Syll. Fung. **4**: 470. 1886; Jour. Myc. **1**: 53. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 63. 1892; B. P. I. Bull. 226: 79. 1912.
452. *C. Sorghi* Ell. & Ev. Jour. Myc. **3**: 15. 1887; Syll. Fung. **10**: 656. 1892; B. P. I. Bull. 226: 51. 1912.
453. *C. sparsa* Cooke, Grev. **12**: 31. 1883; Syll. Fung. **4**: 472. 1886; Jour. Myc. **1**: 51. 1885.
454. *C. sphaeriaeformis* Cooke, Grev. **6**: 140. 1878; Syll. Fung. **4**: 474. 1886; Jour. Myc. **1**: 51. 1885.
455. *C. squalidula* Peck, N. Y. Mus. Rept. **33**: 29. 1880; Syll. Fung. **4**: 431. 1886; Jour. Myc. **1**: 40. 1885; Tuskegee Sta. Bull. **4**: 8. 1904.
456. *C. Stachydis* Ell. & Ev. Torr. Bot. Club Bull. **24**: 474. 1897; Syll. Fung. **14**: 1103. 1899.
457. *C. Stillingiae* Ell. & Ev. Jour. Myc. **3**: 20. 1887; Syll. Fung. **10**: 650. 1892.
458. *C. stomatica* Ell. & Davis, Acad. Phila. Proc. **1895**: 438. 1896; Syll. Fung. **14**: 1102. 1899; Wisc. Acad. Trans. **21**: 275. 1924.
459. *C. Streptopi* Dearn. & Barth. Myc. **9**: 363. 1917.
460. *C. striaeformis* Wint. Hedw. **25**: 103. 1886; Syll. Fung. **10**: 655. 1892.
461. *C. Stylismae* Tracy & Earle, Torr. Bot. Club Bull. **23**: 206. 1896; Syll. Fung. **14**: 1103. 1899.
462. *C. subsanguinea* Ell. & Ev. Jour. Myc. **4**: 4. 1888; Syll. Fung. **10**: 655. 1892; Mo. Bot. Gard. Ann. **14**: 425. 1927.
463. *C. superflua* Ell. & Holw. Jour. Myc. **2**: 2. 1886; Syll. Fung. **4**: 471. 1886.
464. *C. Symphoricarpi* Ell. & Ev. Jour. Myc. **5**: 70. 1889; Syll. Fung. **10**: 645. 1892.
465. *C. Symplocarpi* Peck in Thuem. Myc. Univ. 669. 1877; Syll. Fung. **4**: 477. 1886; Jour. Myc. **1**: 36. 1885; N. J. Agr. Sta. Bull. 313: 142. 1917.
466. *C. tabacina* Ell. & Ev. Jour. Myc. **4**: 6. 1888; Syll. Fung. **10**: 627. 1892; Wisc. Acad. Trans. **20**: 430. 1922.
467. *C. tageticola* Ell. & Ev. Jour. Myc. **8**: 72. 1902; Syll. Fung. **18**: 608. 1906.
468. *C. tenuis* Peck, N. Y. Mus. Rept. **47**: 23. 1894; Syll. Fung. **11**: 627. 1895.
469. *C. Tephrosiae* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 44. 1892; Syll. Fung. **10**: 641. 1892.
470. *C. tessellata* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 59. 1892; Syll. Fung. **10**: 656. 1892.
471. *C. Teucrii* Ell. & Kell. Torr. Bot. Club Bull. **11**: 116. 1884; Syll. Fung. **4**: 446. 1886; Jour. Myc. **1**: 20. 1885; Wisc. Acad. Trans. **21**: 262. 1924.
472. *C. texensis* Ell. & Gall. Jour. Myc. **4**: 116. 1888; Syll. Fung. **10**: 646. 1892.
473. *C. Thaliae* Ell. & Langl. Jour. Myc. **6**: 36. 1890; Syll. Fung. **10**: 654. 1892.
474. *C. Thaspii* Ell. & Ev. in Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 61. 1892.

475. *C. Thermopsidis* Earle, N. Y. Bot. Gard. Bull. **2**: 348. 1902; Syll. Fung. **18**: 600. 1906.
476. *C. tinea* Sacc. Michelia **1**: 268. 1878; Syll. Fung. **4**: 468. 1886; Jour. Myc. **3**: 18. 1887.
477. *C. Torae* Tharp, Myc. **9**: 115. 1917.
478. *C. torta* Tracy & Earle, Torr. Bot. Club Bull. **28**: 187. 1901; Syll. Fung. **18**: 605. 1906.
479. *C. tortipes* Davis, Wisc. Acad. Trans. **20**: 430. 1922.
480. *C. Toxicodendri* Ell. Am. Nat. **16**: 811. 1882; Syll. Fung. **4**: 467. 1886; Jour. Myc. **1**: 62. 1885.
481. *C. Tragopogonis* Ell. & Ev. Torr. Bot. Club Bull. **24**: 474. 1897; Syll. Fung. **14**: 1102. 1899.
482. *C. Tropaeoli* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 59. 1892; Syll. Fung. **10**: 619. 1892.
483. *C. truncata* Ell. & Ev. Jour. Myc. **3**: 19. 1887; Syll. Fung. **10**: 639. 1892.
484. *C. truncatella* Atk. Elisha Mitchell Sci. Soc. Jour. **8**: 44. 1892; Syll. Fung. **10**: 644. 1892.
485. *C. tuberculans* Ell. & Ev. Jour. Myc. **4**: 115. 1888; Syll. Fung. **10**: 652. 1892.
486. *C. tuberculella* Davis, Wisc. Acad. Sci. Trans. **20**: 429. 1922.
487. *C. tuberosa* Ell. & Kell. Torr. Bot. Club Bull. **11**: 116. 1884; Hedw. **23**: 171. 1884, as *C. glaucescens* Wint.; Syll. Fung. **4**: 439. 1886; Jour. Myc. **1**: 38. 1885.
488. *C. umbrata* Ell. & Holw. Jour. Myc. **2**: 2. 1886; Syll. Fung. **4**: 444. 1886; Wisc. Acad. Trans. **14**: 97. 1903; *l. c.* **17**: 895. 1914.
489. *C. unicolor*[1] Sacc. & Penz. Michelia **2**: 642. 1882; Stevens, The Fungi which Cause Plant Disease, p. 631. 1913.
490. *C. vaginae* Kreuger in Mededeel. Proefst. Suiker. **24**: 8. 1896; Syll. Fung. **14**: 1106. 1899; U. S. D. A. Bull. 1366. 1926.
491. *C. varia* Peck, N. Y. Mus. Rept. **35**: 141. 1884; Syll. Fung. **4**: 468. 1886; Jour. Myc. **1**: 63. 1885; Univ. Maine Studies 3^1: 22. 1902; Wisc. Acad. Trans. **18**: 294. 1915; *l. c.* **20**: 422. 1922.
492. *C. variicolor* Wint. Hedw. **24**: 205. 1885; Syll. Fung. **4**: 431. 1886; Jour. Myc. **1**: 124. 1885.
493. *C. velutina* Ell. & Kell. Torr. Bot. Club Bull. **11**: 122. 1884; Syll. Fung. **4**: 439. 1886; Jour. Myc. **1**: 52. 1885; Wisc. Acad. Trans. **19**: 702. 1919; *l. c.* **21**: 258. 1924.
494. *C. venturioides* Peck, N. Y. Mus. Rept. **34**: 47. 1881; Am. Nat. **16**: 810. 1882, as *C. Asclepiadis* Ell.; Syll. Fung. **4**: 451. 1886; Jour. Myc. **1**: 20. 1885, as *C. Asclepiadis* Ell.
495. *C. verbascicola* Ell. & Ev. Jour. Myc. **4**: 3. 1888; Syll. Fung. **10**: 633. 1892.
496. *C. Verbenae-strictae* Peck, N. Y. Mus. Bull. 150: 51. 1911; Wisc. Acad. Trans. **21**: 286. 1924.
497. *C. verbenicola* Ell. & Ev. Jour. Myc. **3**: 19. 1887; Syll. Fung. **10**: 632. 1892; Iowa Acad. Proc. **7**: 165. 1899.
498. *C. Vernoniae* Ell. & Kell. Am. Nat. **17**: 1166. 1883; Syll. Fung. **4**: 443. 1886; Hedw. **24**: 206. 1885; Jour. Myc. **1**: 21. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 46. 1892; Wisc. Acad. Trans. **9**: 168. 1893; *l. c.* **17**: 894. 1914; Cornell Univ. Bull. 3^1: 41. 1897; B. P. I. Bull. 226: 94. 1912.

[1] This species was originally reported on *Laurus nobilis*. The reference to it on a species of *Lilium* might well be questioned.

499. *C. vexans* C. Massal. Ann. Myc. **4**: 494. 1906; Syll. Fung. **22**: 1417. 1913; Wisc. Acad. Trans. **20**: 421. 1922.
500. *C. Viciae* Ell. & Holw. Jour. Myc. **1**: 5, 39. 1885; Syll. Fung. **4**: 438. 1886; Wisc. Acad. Trans. **17**: 892. 1914; *l. c.* **21**: 258. 1924.
501. *C. Vignae* Ell. & Ev. Jour. Myc. **3**: 19. 1887; Syll. Fung. **10**: 621. 1892; B. P. I. Bull. 226: 48. 1912.
502. *C. viminei* Tehon, Myc. **16**: 141. 1924.
503. *C. Vincetoxici* Ell. & Ev. Jour. Myc. **8**: 73. 1902; Syll. Fung. **18**: 609. 1906.
504. *C. Violae* Sacc. Nuovo Giorn. Bot. Ital. **8**: 187. 1876; Syll. Fung. **4**: 434. 1886; Jour. Myc. **1**: 19. 1885; N. Y. Mus. Rept. **38**: 100. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 53. 1892; Field Mus. Bot. Ser. Rept. **1**: 93. 1896; B. P. I. Bull. 226: 89. 1912; N. J. Agr. Sta. Bull. 313: 142. 1917; Wisc. Acad. Trans. **20**: 421. 1922.
505. *C. viridula* Ell. & Ev. Jour. Myc. **5**: 70. 1889; Syll. Fung. **10**: 632. 1892.
506. *C. Viticis* Ell. & Ev. Jour. Myc. **3**: 18. 1887; Syll. Fung. **10**: 648. 1892; B. P. I. Bull. 226: 70. 1912.
507. *C. Vitis* (Lév.) Sacc. in Rab. Fungi Eur. 2150; Ann. Sci. Nat. Bot. III. **9**: 261. 1848, as *Septonema Vitis* Lév.; Syll. Fung. **4**: 458. 1886, as *C. viticola* (Ces.) Sacc.; Hedw. **24**: 206. 1885; Elisha Mitchell Sci. Soc. Jour. **8**: 56. 1892, as *C. viticola* (Ces.) Sacc.; B. P. I. Bull. 226: 34. 1912.
508. *C. vulpinae* Ell. & Kell. Jour. Myc. **3**: 127. 1887; Syll. Fung. **10**: 638. 1892.
509. *C. Weigelae* Ell. & Ev. Acad. Phila. Proc. **1893**: 170. 1893; Syll. Fung. **11**: 628. 1895.
510. *C. xanthicola* Heald & Wolf, Myc. **3**: 20. 1911; B. P. I. Bull. 226: 91. 1912.
511. *C. Xanthoxyli* Cooke, Grev. **12**: 30. 1883; Syll. Fung. **4**: 465. 1886; Jour. Myc. **1**: 34. 1885.
512. *C. Xyridis* Miles, Myc. **18**: 168. 1926.
513. *C. Zeae-Maydis* Tehon & Daniels, Myc. **17**: 248. 1925.
514. *C. zebrina*[1] Pass. Hedw. **16**: 124. 1877; Syll. Fung. **4**: 437. 1886; Jour. Myc. **1**: 39. 1885; Wisc. Acad. Trans. **17**: 892. 1914; *l. c.* **21**: 294. 1924; Myc. **16**: 125. 1924.
515. *C. Zinniae* Ell. & Mart. Jour. Myc. **1**: 20. 1885; Syll. Fung. **4**: 443. 1886; Elisha Mitchell Sci. Soc. Jour. **8**: 42. 1892.
516. *C. Ziziae* Ell. & Ev. Jour. Myc. **3**: 16. 1887; Syll. Fung. **10**: 625. 1892; Wisc. Acad. Trans. **9**: 168. 1892; *l. c.* **17**: 893. 1914.

[1] Note from Wisc. Acad. Trans. **21**: 294. 1924: "The publication of this name seems to antedate that of *C. helvola* Sacc." but Davis in *l. c.* **19**: 675. 1919, notes that "*C. zebrina* Pass. is referred to *C. helvola* Sacc. as a variety by Ferraris (Fl. Ital. Crypt. **1**: 8, 423)."

Host Families and Their Cercosporas

The name of the family is followed by a number which refers to the species number as given in the "Index to Species of Cercospora."

Acanthaceae—118, 145.
Aceraceae—326.
Alismaceae—15, 352, 421.
Amaranthaceae—7, 16, 63, 73, 124.
Amaryllidaceae—20, 354.
Anacardiaceae—53, 250, 405, 406, 480.
Anonaceae—41.
Apocynaceae—32, 330, 401.
Aquifoliaceae—246, 247, 390.
Araceae—70, 352, 465.
Araliaceae—22, 47, 269.
Asclepiadaceae—40, 54, 66, 100, 164, 225, 248, 249, 494, 503.
Begoniaceae—*C.* sp.
Berberidaceae—85, 376.
Bignoniaceae—75, 82, 159, 261, 451.
Boraginaceae—228.
Campanulaceae—161.
Capparidaceae—102, 119.
Caprifoliaceae—27, 83, 140, 147, 264, 464, 476, 491, 509.
Caryophyllaceae—315, 316.
Celastraceae—143, 177, 303.
Chenopodiaceae—26, 55, 157, 191.
Compositae—1, 12, 13, 25, 36, 43, 45, 52, 56, 68, 80, 93, 95, 98, 101, 106, 148, 155, 162, 165, 171, 176, 178, 184, 197, 213, 214, 219, 221, 226, 227, 238, 259, 291, 301, 310, 335, 339, 340, 342, 351, 361, 383, 395, 396, 398, 409, 419, 432, 443, 444, 458, 466, 467, 481, 488, 498, 502, 510, 515, 522.
Convolvulaceae—*C.* sp., 14, 120, 252, 461, 486, 505.
Cornaceae—121, 122, 202, 211, 338.
Crassulaceae—429, 430.
Cruciferae—39, 46, 59, 129, 173, 268, 325, 521.
Cucurbitaceae—*C.* sp., 99, 131, 161.
Cyperaceae—77, 78, 125, 309.
Dioscoreaceae—151, 336.
Dipsaceae—167.
Ebenaceae—44, 152, 153, 192, 196, 257.
Elaeagnaceae—163.
Ericaceae—37, 168, 169, 203, 258, 350, 453.
Euphorbiaceae—3, 4, 38, 73, 74, 81, 126, 127, 128, 179, 180, 181, 234, 251, 254, 297, 298, 388, 389, 410, 457.
Fagaceae—290, 379.
Gentianaceae—182, 206, 207, 329, 420.
Geraniaceae—67, 208.
Gramineae—13, 69, 160, 199, 215, 321, 347, 355, 427, 431, 437, 439, 440, 452, 460, 470, 490, 513.
Hamamelidaceae—485.
Hydrophyllaceae—324.
Hypericaceae—244.
Juglandaceae—224, 255.
Labiatae—166, 184, 253, 267, 284, 299, 306, 328, 395, 423, 428, 456, 471.
Lauraceae—*C.* sp., 345, 393, 447.
Leguminosae—47, 73, 89, 90, 91, 103, 109, 112, 115, 130, 134, 136, 139, 141, 142, 156, 174, 175, 187, 190, 200, 212, 223, 229, 230, 245, 263, 265, 266, 270, 278, 281, 282, 300, 302, 317, 320, 334, 341, 345, 357, 363, 364, 365, 371, 384, 445, 446, 469, 475, 477, 487, 493, 500, 501, 507, 514, 520.
Liliaceae—42, 84, 113, 193, 231, 294, 447, 448, 449, 459, 462, 489.
Linaceae—274.
Lobeliaceae—162, 277.
Loganiaceae—478.
Lythraceae—21, 137, 286, 287, 331.
Magnoliaceae—276, 293.
Malvaceae—2, 17, 18, 19, 64, 217, 236, 237, 260, 295, 314, 441, 517.
Marantaceae—473.
Martyniaceae—55.
Melastomaceae—176.
Meliaceae—271, 304.
Menispermaceae—305.
Moraceae—61, 185, 186.
Myricaceae—148, 154, 323, 359.
Nyctaginaceae—313, 349.
Nymphaeaceae—183, 327, 337.

Oleaceae—8, 92, 194, 195, 272, 273, 280, 292, 463, 472.
Onagraceae—146, 170, 204, 205, 256, 279, 318, 343, 344.
Orchidaceae—133.
Papaveraceae—424.
Passifloraceae—57, 198, 400, 484.
Phytolaccaceae—189.
Pinaceae—435, 436.
Piperaceae—426.
Plantaginaceae—372, 373.
Platanaceae—374.
Polemoniaceae—346, 366.
Polygalaceae—220.
Polygonaceae—5, 6, 50, 51, 172, 222, 243, 377, 404, 415, 438.
Polypodiaceae—72, 367.
Pontederiaceae—370, 380.
Primulaceae—285.
Punicaceae—286.
Ranunculaceae—33, 188, 307, 353, 397, 417, 455, 492, 519.
Resedaceae—402.
Rhamnaceae—9, 86, 288, 403.
Rosaceae—31, 58, 88, 94, 97, 111, 116, 117, 132, 233, 296, 312, 385, 394, 412, 413, 414, 416, 417, 418, 434, 499.
Rubiaceae—62, 87, 96, 105, 149, 150, 201, 232, 239, 362, 392, 468.
Rutaceae—11, 49, 387, 511.
Salicaceae—381, 382, 399, 422.
Santalaceae—60, 107, 110.
Sapindaceae—10.
Sapotaceae—262.
Saxifragaceae—*C.* sp., 24, 34, 104, 138, 144, 235, 240, 241, 407, 408.
Scrophulariaceae—*C.* sp., 100, 209, 218, 311, 360, 479, 495.
Simurabaceae—210.
Solanaceae—*C.* sp., 48, 73, 76, 79, 114, 123, 130, 135, 148, 158, 283, 332, 333, 368, 369, 411, 450.
Tiliaceae—308.
Tropaeolaceae—482.
Umbelliferae—*C.* sp., 23, 28, 29, 30, 242, 348, 358, 375, 378, 425, 442, 474, 516.
Urticaceae—289, 319, 391, 454, 518.
Verbenaceae—71, 275, 356, 433, 496, 497, 506.
Violaceae—108, 216, 322, 504.
Vitaceae—22, 35, 65, 386, 483, 507, 508.
Xyridaceae—512.

Addenda

Althaea rosea Cav.

517. *C. nebulosa* Sacc. Nuovo Giorn. Bot. Ital. **8**: 189. 1876; U. S. D. A. Bull. 1366. 1926.

Celtis?

518. *C. Spegazzinii*[1] Sacc. Syll. Fung. **4**: 475. 1886; Fung. Fl. Kansas p. 10. 1927.

Delphinium spp.

519. *C. Delphinii* Thuem. Bull. Soc. Imp. Nat. Moscou **55**: 75. 1880; Syll. Fung. **4**: 432. 1886; U. S. D. A. Bull. 1366. 1926.

Glycine Max Merr.

520. *C. diazu* Miura, Bull. So. Manchurian Ry. Co., Agr. Exp. Sta.[2] **11**: 1921; Jour. Agr. Res. **33**: 393. 1926; *l. c.* **36**: 827. 1928.

Martynia louisiana Mill.

521. *C. decolor*[1] Pass. Syll. Fung. **4**: 448. 1886; Fung. Fl. Kansas p. 8. 1927.

Solidago serotina Ait.

522. *C. fulvescens* Sacc. Nuovo Giorn. Bot. Ital. **8**: 189. 1896; Syll. Fung. **4**: 445. 1886; Fung. Fl. Kansas p. 9. 1927.

[1] The original citations have not been available for verification and are therefore omitted.

[2] The English abstract in the Jap. Jour. Bot. **1**[1]: (9). 1922, indicates this as the original place of description.

STUDIES ON THE GROWTH OF ROOT HAIRS IN SOLUTIONS

IX. THE pH-MOLAR RATE RELATION FOR COLLARDS IN CALCIUM NITRATE

CLIFFORD H. FARR

Late Associate Professor of Botany in the Henry Shaw School of Botany of Washington University

A preliminary study of the growth of root hairs of collards in calcium nitrate, reported in No. II of this series,[1] represented an attempt to analyze the effect produced by increasing the concentration of the salt in the culture solution. The two separable factors in evidence were the chemical effect of the salt and the osmotic effect of the solution. In a solution containing 0.003 *M* sucrose, in addition to the optimum concentration of calcium nitrate, there was the same amount of retardation in growth that was obtained through the addition of an equimolar concentration of calcium nitrate. If, however, these additions were made to suboptimal concentrations of calcium nitrate, there was a decrease in the percentage of retardation due to sucrose and a positive acceleration upon the addition of equimolar amounts of nitrate. It seemed probable therefore that the effect of osmotic pressure alone was retardation, but that in this latter instance it had been overcome by the stimulative property of the calcium nitrate up to a certain concentration.

[1] Farr, C. H. Studies on the growth of root hairs in solutions.

I. The problem, previous work, and procedure. Am. Jour. Bot. **14**: 446–456. *f. 1.* 1927.

II. The effects of concentration of calcium nitrate. *Ibid.* 497–515. *f. 2.* 1927.

III. The effects of concentrations of $CaCl_2$ and $Ca(OH)_2$. *Ibid.* 553–564. *f. 3–4.* 1927.

IV. The pH-molar-rate relation for collards in calcium chlorid. *Ibid.* **15**: 6–31. *f. 5–10.* 1928.

V. Root hair elongation as an index of root development. *Ibid.* 103–113. *f. 11–15.* 1928.

VI. Structural responses to toxic pH and molar concentrations of calcium chlorid. *Ibid.* 171–178. *pl. 7–9.* 1928.

VII. Further investigations on collards in calcium hydroxide. Torr. Bot. Club Bul. **55**: 223–245. *f. 16–18.* 1928.

VIII. Structural and intracellular features of collards in calcium nitrate. *Ibid.* **55**: 529–553. 1928.

It was suggested by the author that the critical concentration represented by the optimum of the graph might be due to a limiting factor with respect to the amount of calcium which could be absorbed from the solution, modified by the negative effect of the osmotic pressure. The nitrate ion was mentioned as a possible controlling agent in the determination of the amount of calcium absorbed. The addition of calcium nitrate above the optimal concentration could not, then, increase the rate of growth, and the retardative effect of osmotic pressure was shown in the downward slope of the curve. The sharp break in the curve in the region of optimum concentration marked the point where the accelerative effect of calcium nitrate ended and the retardative effect of osmotic pressure began. The gradual slope of the curve in solutions of still higher osmotic pressure was thought to be due to the gradual adjustment of the root hairs to the solutions.

Because of the peculiar relationship of calcium to the growth produced in solutions of varying acidity or alkalinity, it became necessary to determine the pH of every solution used. The present study represents a more complete observation of the behavior of the root hairs in different concentrations of calcium nitrate in hydrogen-ion concentrations varying from 3.5 to 12.0.

The experiments were carried on at the Marine Biological Laboratory, Woods Hole, Mass. The methods and procedure were essentially the same as those described in paper No. IV, of the series noted above. In this present study, however, buffer solutions were obtained which would cover more completely the upper part of the pH range in order to increase the accuracy of the colorimetric determinations from pH 9.5 to pH 12.0. To the series of indicators previously used there were added Brom Cresol Green, Nitro Yellow (pH 10.0–11.6), and Sulpho Orange (pH 11.0–12.6). The entire series of standard solutions with the respective indicators were placed upon a rotating table in order to increase the facility and rapidity with which the colorimetric determinations could be made. Pyrex glass tubing, stop-cocks, and separatory funnels were used as well as the Pyrex flasks for the solutions. A filter pump was employed for aeration instead of the aspirator bottles used formerly. Solutions of the desired concentration of calcium nitrate were prepared from a 0.5 *M*

stock solution, and the acidity or alkalinity was adjusted to the desired point by the addition of either nitric acid or calcium hydroxide.

pH	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5
0.100			13.4						18.4					1.1		
0.050		16.6			26.6		25.6				25.9				8.6	
0.030			11.0		34.0		51.3		51.5		30.0	27.3		32.1	28.4	0.0
0.020		12.3			17.2		39.7		62.2		31.6		47.0		25.8	
0.012	0.0		56.2		54.9		72.5		53.9		27.6		54.7	41.6	7.9	
0.008		15.5			64.4		54.7		76.1		57.8		26.3	21.8		
0.004			14.1		53.2		54.2	72.1	64.1		59.2		61.3		49.5	0.0
0.000							0.0	51.0	62.9	39.6	45.2	36.9	85.6		37.4	4.5
Mols.																

TABLE I

Average root-hair elongation in calcium nitrate.

In table I is given a summary of the average rate of root-hair elongation in concentrations of calcium nitrate varying from 0.004 *M* to 0.100 *M* and covering a pH range of 4.0–11.5. This same data is presented in more graphic form in fig. 1. A com-

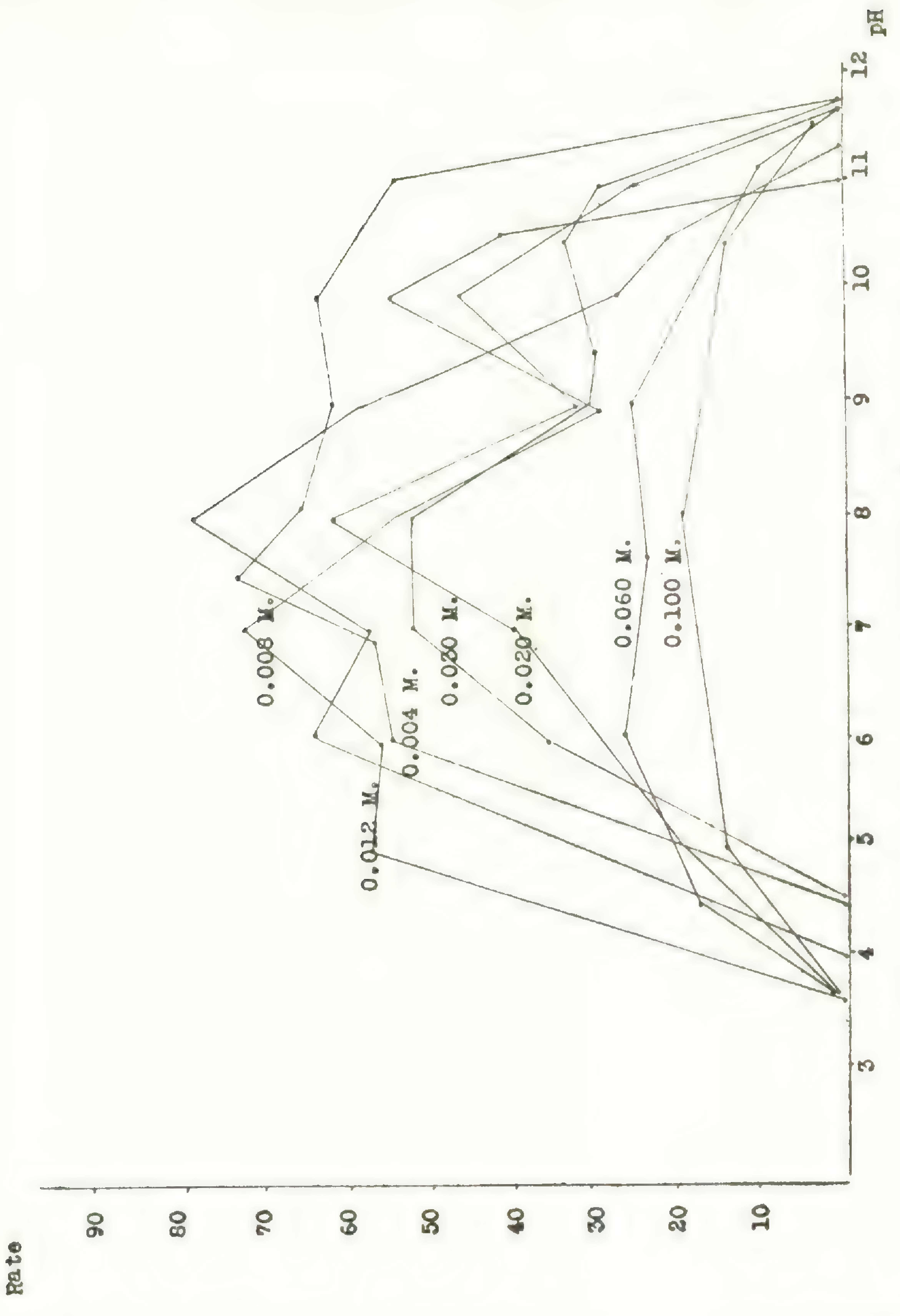

Fig. 1. Average rate of root-hair elongation in calcium nitrate.
C. H. Farr, 1927.

parison of these results with those obtained in solutions of calcium chloride under similar conditions shows a very close agreement. The pH range covered is essentially the same. All curves for the average rate of root-hair elongation in calcium chloride were

bimodal with the exception of those in the higher concentrations. These were monomodal in form. In calcium nitrate there are three types of curves, the trimodal in lower concentrations, the bimodal in median concentrations, and the monomodal in higher concentrations. Increase in the concentration of the salt brought about a decrease in the range of acidity and alkalinity which would support growth in both calcium chloride and calcium nitrate. The highest average rate of growth in calcium chloride occurred at a concentration of 0.008 *M* and at a pH of 7.9. The highest average rate of growth in calcium nitrate occurred at a concentration of 0.008 *M* and at a pH of 8.0. The numerical value of this highest average rate in calcium chloride is 88.4, in calcium nitrate, 76.1. This tendency in all solutions of calcium chloride to support a slightly higher rate of growth than that which took place in equimolar solutions of calcium nitrate is obvious. The difference is so small, however, that it may be of no significance. It will be discussed in another connection later.

The maximum rates of root-hair elongation are summarized in table II. These values are obtained from the highest rate of growth attained by any root hair at the pH indicated in the solutions of various concentrations. In calcium nitrate the most rapid growth occurred at a concentration of 0.012 *M* at a pH of 7.0. Similar data in solutions of calcium chloride show the most rapid growth of any individual hair to have taken place at a concentration of 0.020 *M* and at a pH of 6.9.

Many considerations in connection with these curves become clearer when they are presented in terms of three dimensions (fig. 2). This model is based upon fig. 1 and the curve for growth rate in calcium hydroxide. The median or neutral optimum found in calcium nitrate is shown here to be slightly zig-zag. It may be assumed, however, that if the data had been obtained at a pH of 7.5 instead of at 7.0 and 8.0 in the median concentrations that this would have been a straight line also.

The idea advanced in previous papers of the series that the rate of elongation of the root hairs represents an accurate index of the development of the root in general is further substantiated by the findings in solutions of calcium nitrate. Four factors may be compared with respect to the influence of the salt and the pH

of the solution, at each of the concentrations used. In a low concentration of calcium nitrate (0.004 *M*) a fairly close correspondence is found between root and root-hair elongation (fig. 3). The upper curve represents the maximum rate of root-hair elon-

pH	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5
0.100			26.2						28.1					2.2		
0.060		35.8			42.0		37.4				39.5				20.9	
0.030			34.3		59.1		69.3		90.1		58.4	56.0		46.7	46.7	0.0
0.020		38.9			46.0		59.7		93.2		63.1		81.4		50.7	
0.012	0.0		71.3		71.5		94.7		77.7		58.1		71.5	65.3	16.6	
0.008		33.3			75.8		78.6		89.4		84.8		68.4	57.5		
0.004			41.1		69.3		67.1	83.9	83.9		80.8		87.9		76.4	0.0
0.000							0.0	62.8	80.1	70.5	55.0	66.2	114.1		57.5	14.1
Mols.																

TABLE II

Maximum root-hair elongation in calcium nitrate.

gation, the next the average rate of root-hair elongation, the third is based upon root elongation, and the last upon the maximum length of root hairs. Root elongation here gives a trimodal

Fig. 2. Three-dimensional graph of the maximum rate of growth of root hairs of collards in calcium nitrate. Vertical parallel lines indicate pH units. Horizontal graphs refer to respective molar concentrations. Uprights represent rate of root-hair elongation. The median vertical line indicates the approximate location of neutrality. The area to the left of this line represents the acid range and the area to the right the alkaline range. The surface bounded by the broad vertical lines indicates the approximate acid and alkaline limits of growth in calcium nitrate. The surface bounded by the converging dark lines represents these same limits in calcium chloride.

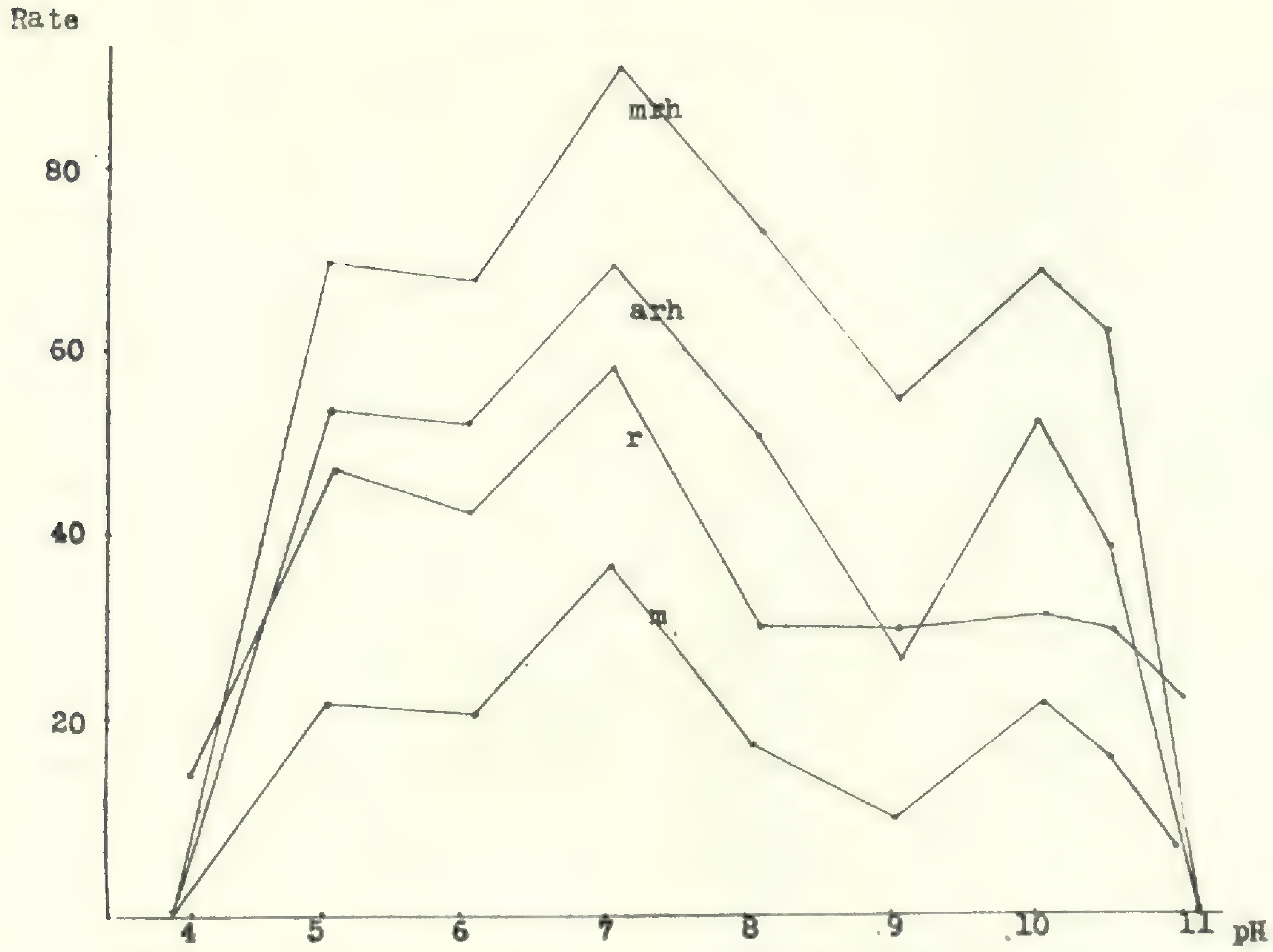

Fig. 3. Root (r) and root-hair elongation in 0.004 *M* calcium nitrate.
C. H. Farr, 1927.

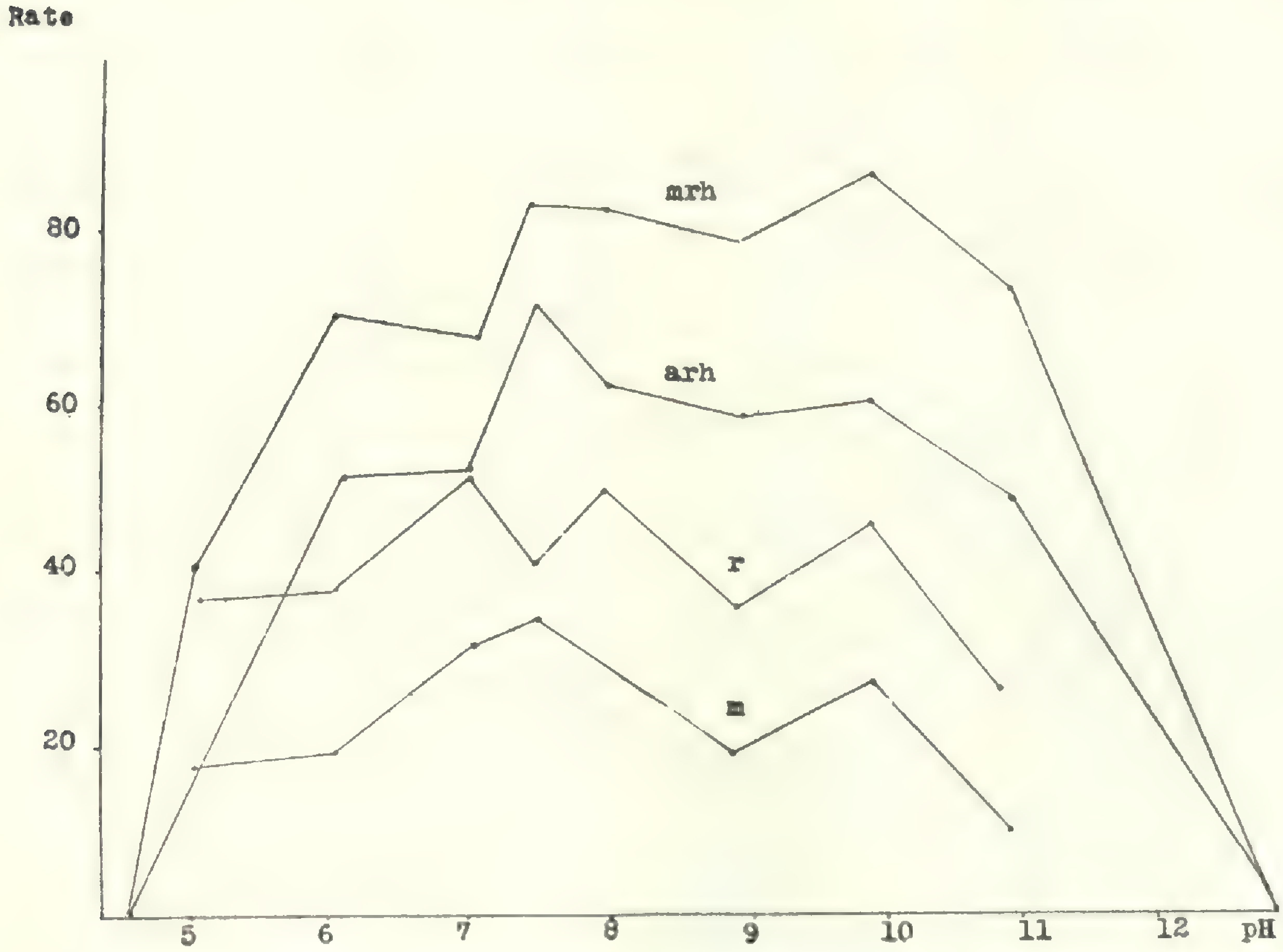

Fig. 4. Root (r) and root-hair elongation in 0.012 *M* calcium nitrate.
C. H. Farr, 1927.

curve such as was obtained for root-hair elongation. The locations of the modes do not, however, correspond except in the alkaline optima. The curve for maximum length of root hairs is bimodal at this concentration.

A concentration of 0.012 *M* calcium nitrate gives more consistent results (fig. 4). The four graphs are almost identical. The root, however, does not give as good differentiation in the alkaline solutions.

In fig. 5, based upon the results in a solution of 0.020 *M* calcium nitrate, there is again a close similarity in the four graphs.

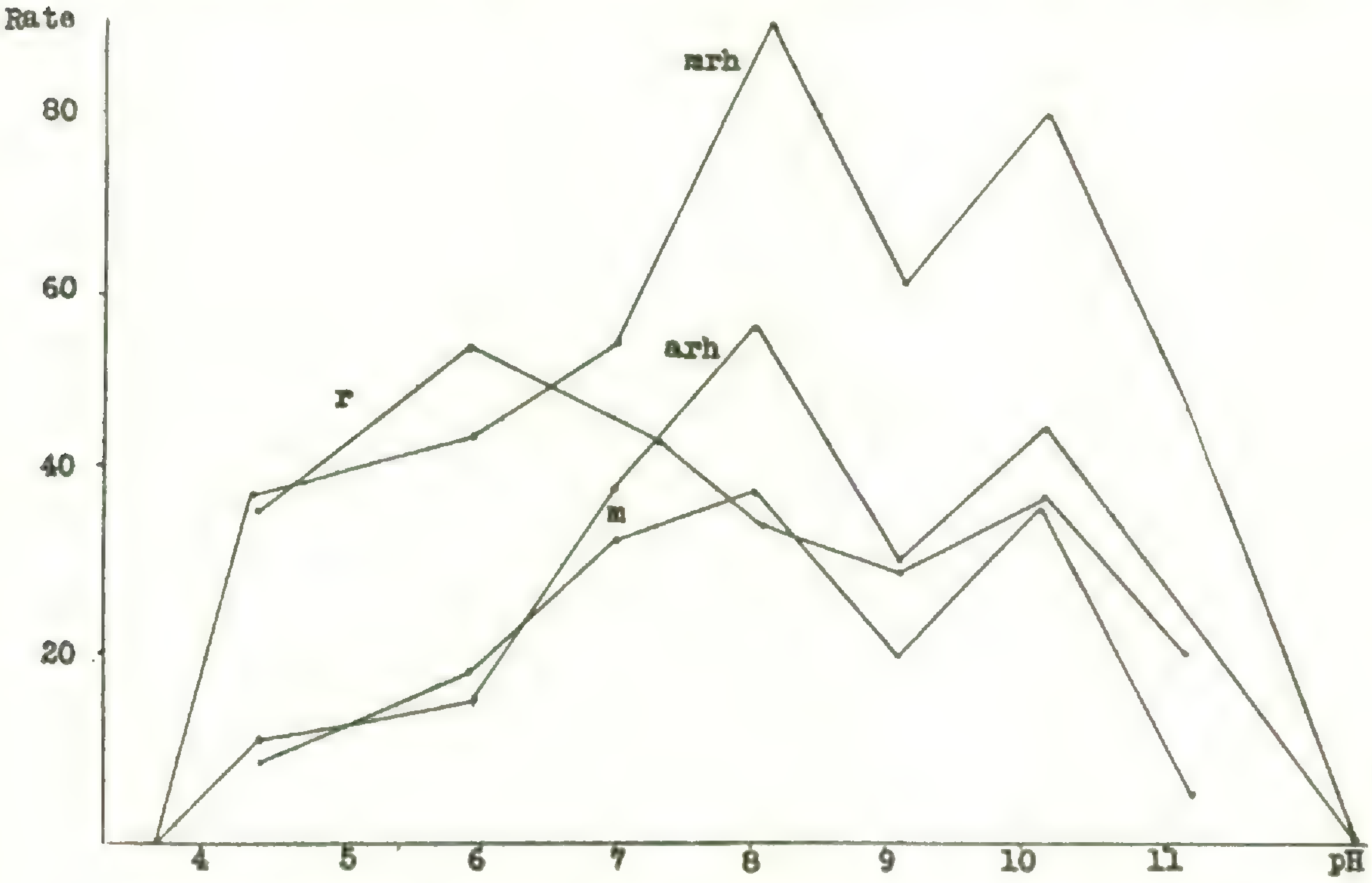

Fig. 5. Root (r) and root-hair elongation in 0.020 *M* calcium nitrate.
C. H. Farr, 1927.

In this instance, however, the acid optimum for the root is at pH 6.0 instead of at pH 8.0 as in the root-hair graphs.

In paper No. IV of this series there was presented in fig. 10 an idealized floor-plan of the three-dimensional graph for the elongation of root hairs in calcium chloride. This graph is shown again in the present study (fig. 6) for the purpose of comparison with the results in calcium nitrate (fig. 7). The median vertical lines in these floor-plans indicate the approximate locations of neutrality. The boundary lines on the right-hand sides represent the alkaline limits of root-hair elongation. The boundary lines

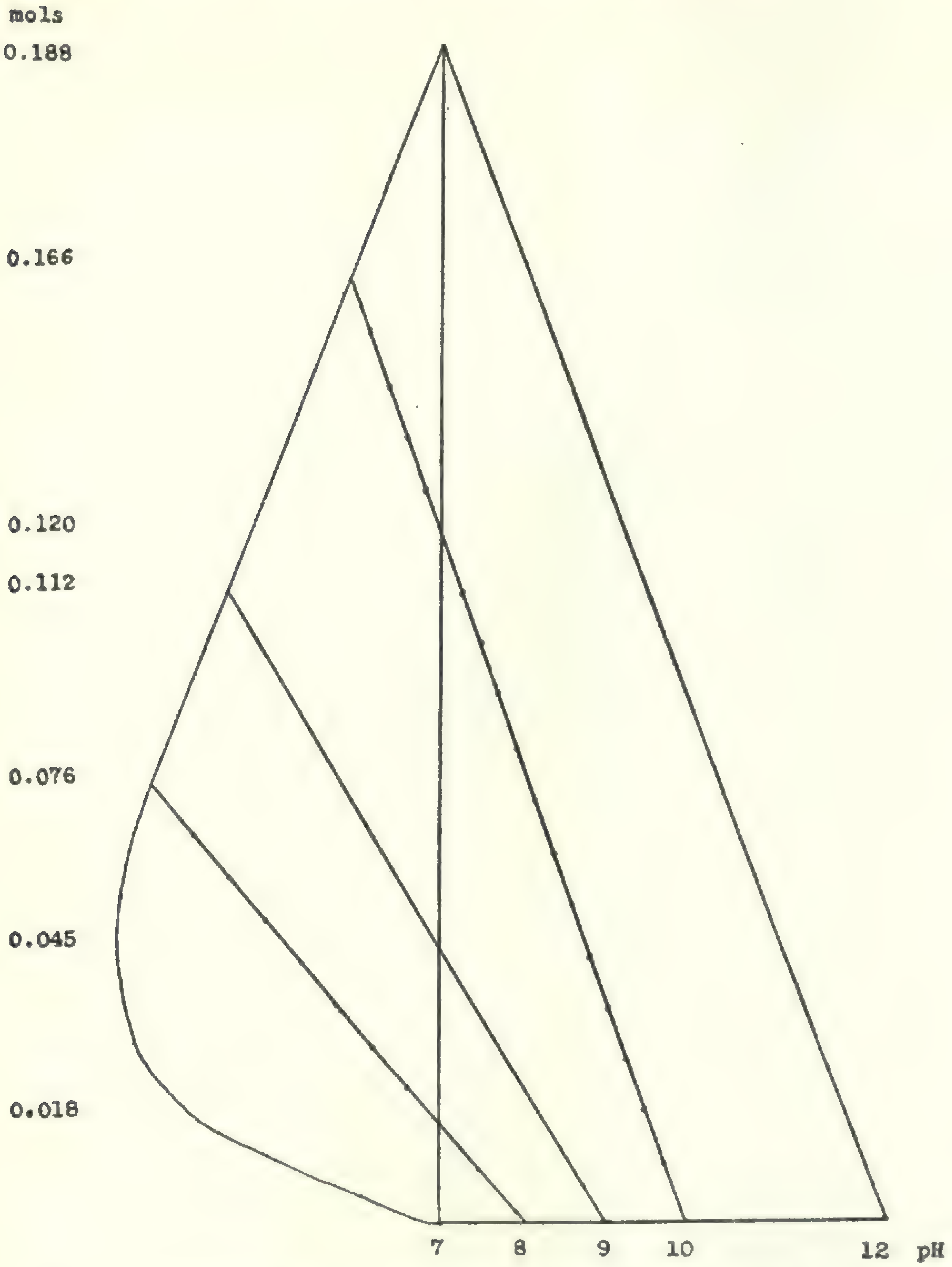

Fig. 6. Tolerance map for collards in calcium chloride solutions of different molar and pH concentrations, based on rate of root-hair elongation. Dotted lines are optima.

on the left-hand side represent the acid limits of root-hair elongation. The oblique lines near to the alkaline limits represent

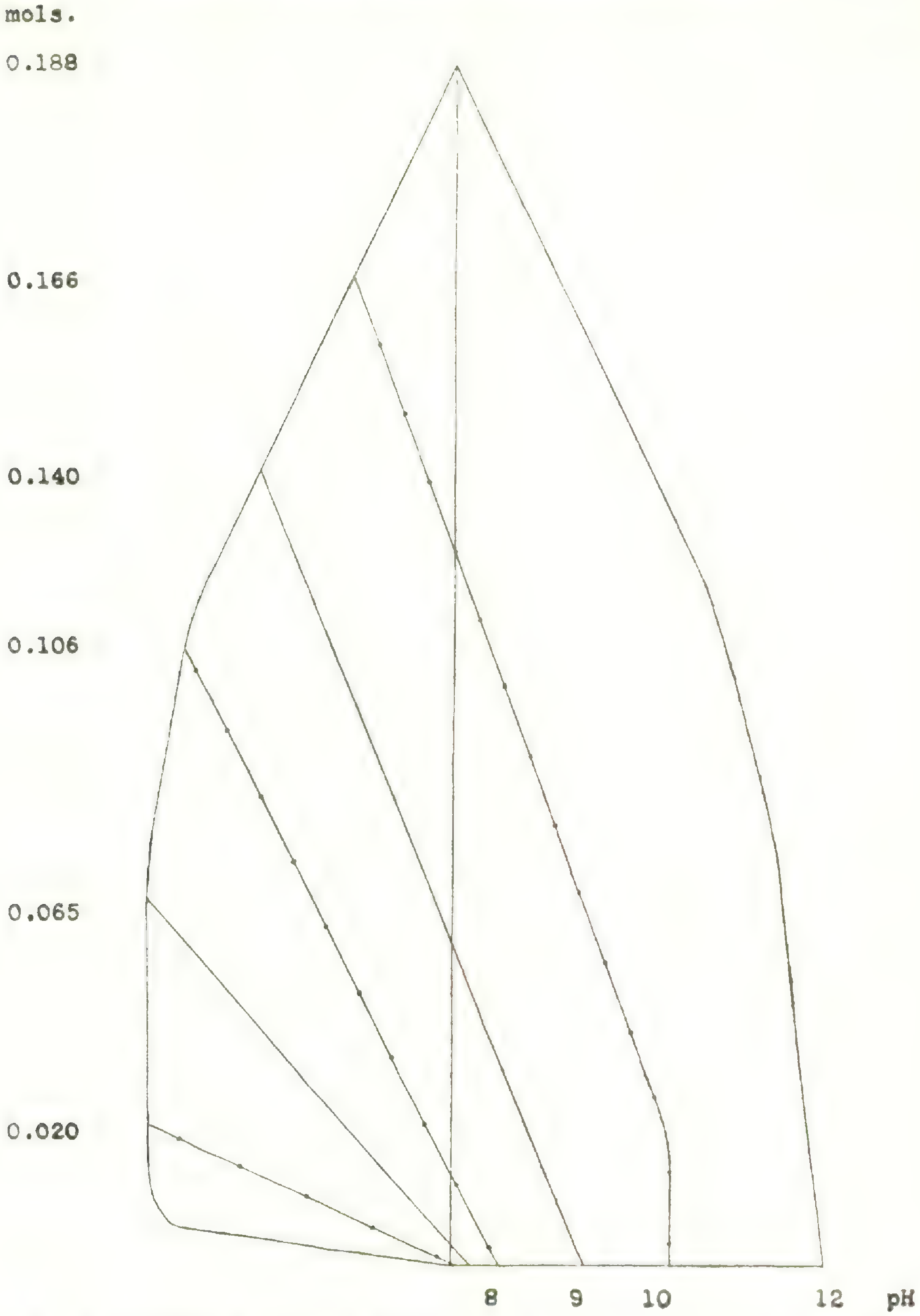

Fig. 7. Idealized floor-plan of tri-dimensional graph for calcium nitrate. Dotted line (——•——•——) indicates maxima.

the alkaline optima. The oblique lines near to the acid limits represent the acid optima. In the graph for calcium chloride the

line between the acid and alkaline optima represents the median minimum. The trimodal graph for calcium nitrate has also a neutral optimum with two minimal regions, the one on the acid and the other on the alkaline side of this central modal location. In both instances the floor-plans are seen to take the general form of an isosceles triangle, with the weak acid corner truncated and curved. It has been pointed out previously that root hairs will not grow in the absence of calcium, hence no growth would be expected in hydrochloric acid in the region represented by the projection of the base line to the left of pH 7.0. It has been known also, from various sources, that calcium antagonizes the injurious effects of the hydrogen ion. These floor-plans clearly show that very dilute calcium solutions which are only slightly acid will not permit root-hair growth. One may observe that appreciable concentrations, 0.018 *M* in the case of calcium chloride and 0.020 *M* in the calcium nitrate, will not permit the production of root hairs in solutions of pH 3.5. A graphic representation is given of the fact that the addition of lime to an acid solution or to a soil low in calcium will alter the solution so that it will support optimum growth conditions, since it changes the pH toward or to neutrality and at the same time raises the calcium content.

Some interesting relationships are brought out by superimposing the floor-plan for calcium nitrate upon that for calcium chloride, (fig. 8). Here it is seen that at most concentrations the plant will produce root hairs in a more alkaline solution of nitrate than of chloride. In weak solutions nitrate will support root-hair growth better than will chloride on the acid side of neutrality. In moderate concentrations root hairs will grow in more acid solutions of chloride than of nitrate. It is shown also that the optima of the two salts bear a definite relation to each other, and that in the nitrate, the shifting of both the acid and the alkaline optimum toward the alkaline side and the pushing of the acid limit toward lower acid concentrations make possible the insertion of a new acid optimum.

The differences which have been pointed out between the results obtained in calcium chloride and in calcium nitrate are, however, very slight and may be without significance. The effects pro-

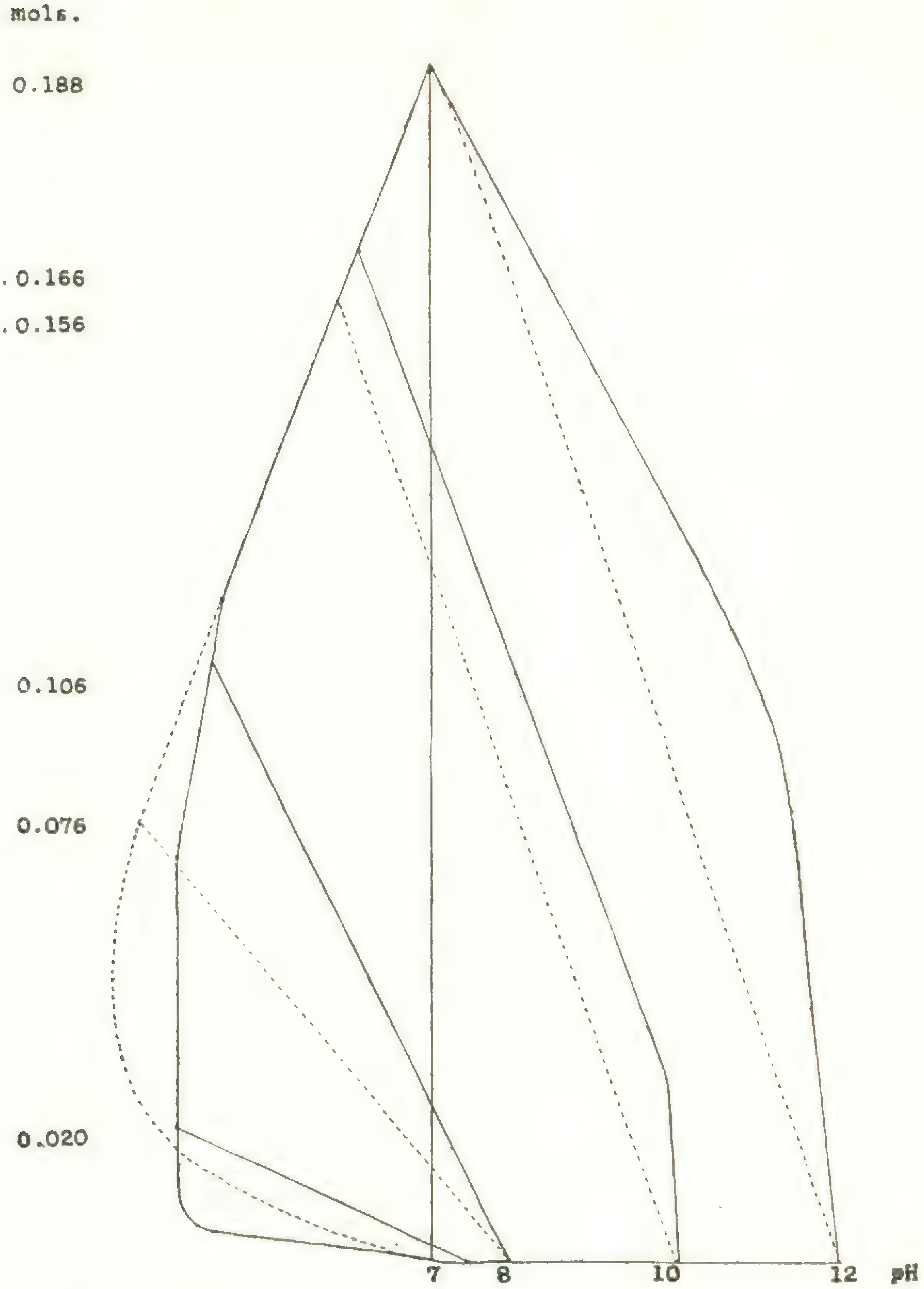

Fig. 8. Floor-plan for calcium nitrate (——) superimposed on calcium chloride (- - - -).

duced by the anions in the two instances are probably more striking because of their similarities than because of their differences.

Further analysis of the entire mass of data obtained for calcium hydroxide, calcium chloride, and calcium nitrate with respect to the possible effects of the anions concerned brings out an interesting correlation. A comparison of the data for the maximum rate of root-hair elongation may be seen in the following table:

Salt	Opt. molar conc.	pH	Max. rate elong.
$Ca(OH)_2$	0.000045	10.0	114.1 microns per hour
$CaCl_2$	0.020	6.9	109.8 microns per hour
$Ca(NO_3)_2$	0.012	7.0	94.7 microns per hour

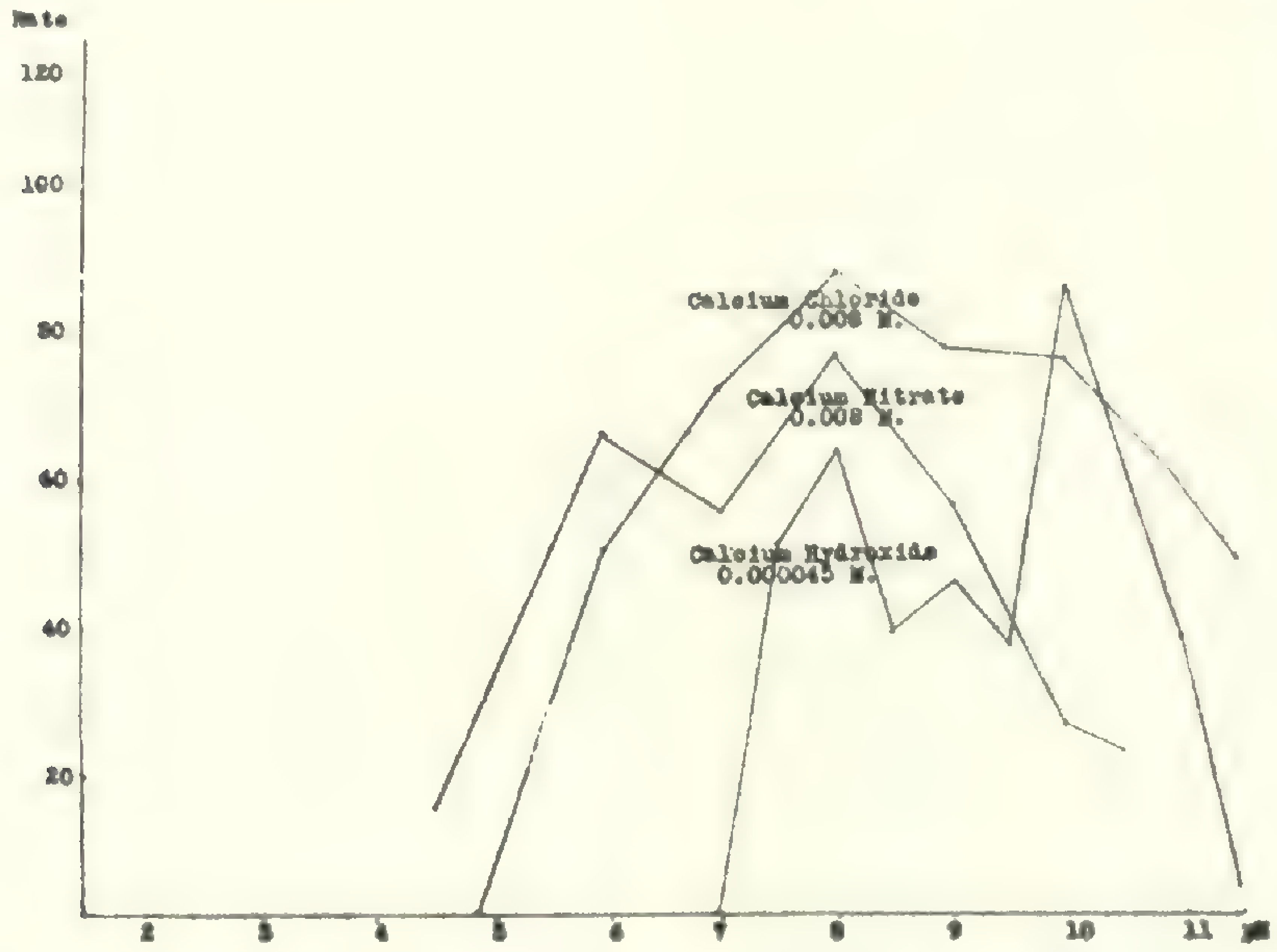

Fig. 9A. Average root-hair elongation in calcium hydroxide, calcium chloride, and calcium nitrate.

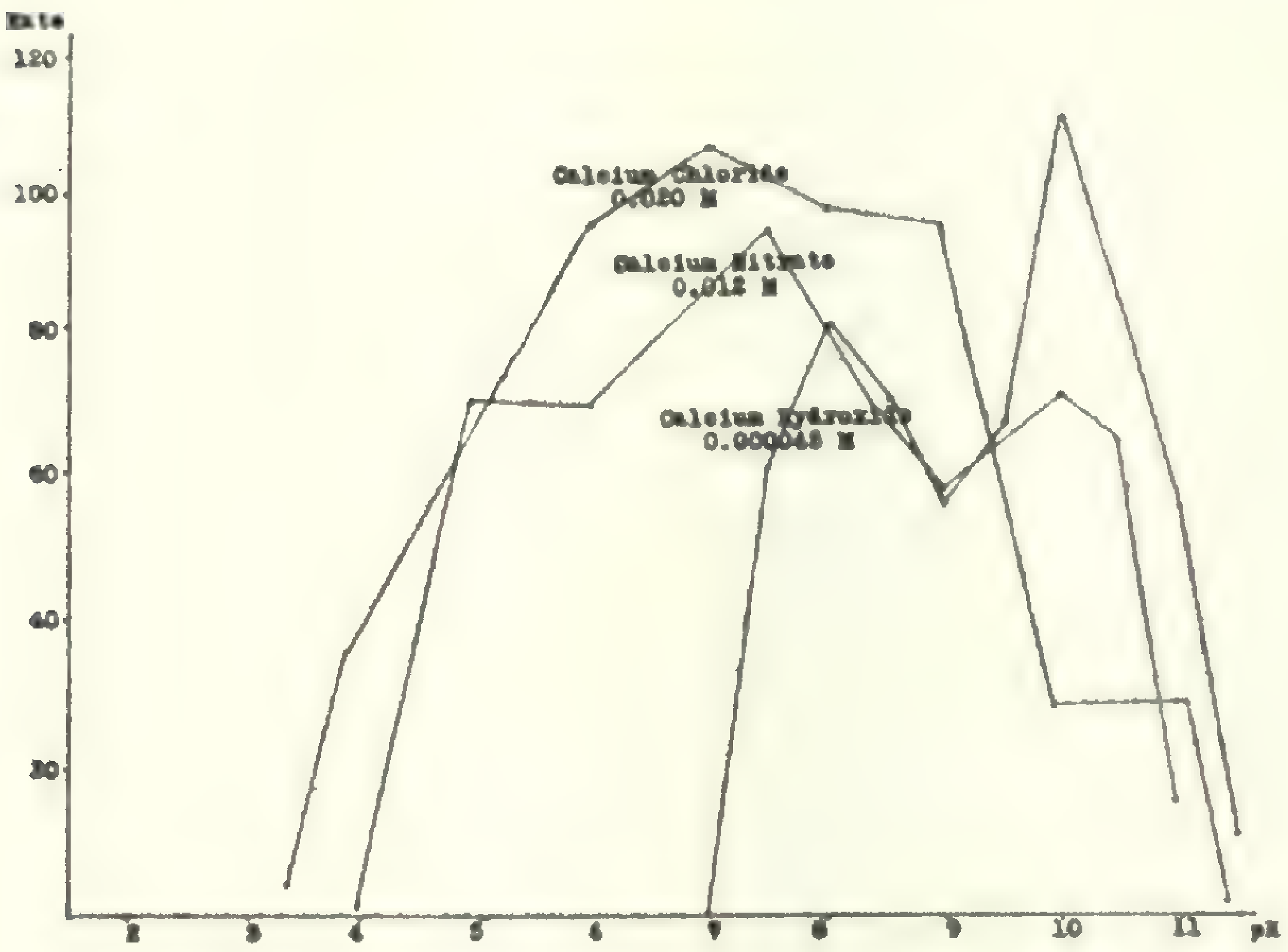

Fig. 9B. Maximum root-hair elongation in calcium hydroxide, calcium chloride, and calcium nitrate.

It is surprising to find that the maximum rate of growth occurred in a 0.000045 *M* solution of calcium hydroxide, noted earlier in No. IV of the series, while the next highest rate of growth occurred in a 0.020 *M* solution of calcium chloride. The latter solution was over 400 times as concentrated with respect to the common cation, calcium. While searching for a possible explanation upon the basis of the effects of the three anions, it became apparent that there is a possible correlation between the absolute velocities of the anions concerned and the different rates of elongation.

Since the solutions employed are exceedingly dilute, the calculations of absolute velocities may be based upon the transference numbers of the ions, the equivalent conductance at infinite dilution, and the Faraday. From the formula,

$$v = \frac{n_a \lambda_0}{F}$$

the values for the three anions are as follows:[1]

OH^{+} = 0.001802 cms. per second

Cl^{-} = 0.000676 cms. per second

NO^{-}_{3} = 0.000638 cms. per second

A comparison of these values with the rates of growth in solutions containing these anions shows a serial relationship which may be of no real significance, but which seems to be worthy of mention. The six curves for the maximum and average rates of root-hair elongation in calcium hydroxide, calcium chloride, and calcium nitrate (fig. 9) are no more striking, but represent the general tendency of the calcium chloride to support a higher rate of growth than did the calcium nitrate. The calcium hydroxide, while containing much less nutritive material and covering a much more narrow pH range, supported the highest rate of growth of all at a pH of 10.0. The fact that more dilute solutions of calcium chloride and calcium nitrate than the 0.020 *M* and 0.012 *M* respectively caused a reduction in growth rate indicates more strongly a possible effect of the anions concerned.

The studies now in progress of the growth rate of root hairs of collards in calcium sulphate may throw some additional light upon the anionic effect. If there is a real correlation between the absolute velocity of the anion in the solution and the rate of growth supported by the solution, the values obtained for calcium sulphate should fall between those for calcium hydroxide and calcium chloride.

WANDA K. FARR.

GENERAL OBSERVATIONS UPON THE ROOT

In addition to the measurement of root-hair elongation a record was kept, throughout the experiments, of the average increase in root length, the average increase in tip length, the length of the zone of aquatic root hairs upon both affluent and effluent sides of the root, the length of the interzone between the aquatic and amphibious root hairs upon both affluent and effluent sides, the

[1] Noyes, A. A., and Falk, K. G. The properties of salt solution in relation to the ionic theory. Am. Chem. Soc. Jour. **34**: p. 454. 1912.

average spacing of the root hairs, and the curvature of the roots in response to the different solutions used. A typical record sheet is shown in table III, in this instance the values obtained in a concentration of 0.060 *M* at pH concentrations of 5.0, 6.0, 7.0, 9.0, and 11.0. A summary of the records, representing in each instance the average of the numerical values obtained for six roots, is given for all of the concentrations studied in table IV. With few exceptions the increase in root length in the lower concentrations is seen to be low in the high acid and high alkaline ranges and to be highest in the region of neutrality. As the concentration of the salt increases, 0.020 *M* and 0.030 *M*, the antagonism of the calcium ion for the hydrogen ion asserts itself and the increase in root length in the acid solutions approaches or equals that in the more neutral solutions. The effect of toxic concentration of the salt has begun to assert itself in the 0.060 *M* solution to the extent that the root development is, in general, suppressed, although there remains an effect of the antagonism of the calcium ion for the hydrogen ion. The data above 0.060 *M* is indicative of the same conditions but it is not extensive enough to be compared with that from the lower concentrations.

The values for average increase in length of the hairless tip, table IV, measured at the beginning and at the end of the experiment each day, are rather irregular. The roots are seen to be well covered with hairs toward the tip in the more neutral solutions in every instance, however. The variations may be accounted for upon the basis of the many factors which are undoubtedly concerned, the toxicity of high concentrations of both the hydrogen and hydroxyl ions, the osmotic effects of concentration of the salt, the individual reactions of the roots studied, etc.

The length of the zone of root hairs shows more consistent results (table IV). The optimum neutral regions present, in every concentration which will permit comparisons with respect to this factor, the larger zones. The lengths of the zones upon the affluent and effluent sides of the root are more nearly equal in the acid and neutral solutions than in the alkaline. This indicates the degree of toxicity of the hydroxyl ion in high concentrations as shown by the delicate reaction of root-hair production.

The data for the presence and extent of an interzone or hair-

TABLE III

ROOT DEVELOPMENT IN CALCIUM NITRATE (0.060 *M*)

pH	Root No.	Root		Tip		Zone		Interzone		Space	Curv.	
		o	l	o	l	t	f	t	f		o	l
	A1	5.0	9.0	1.5	4.5	0.0	0.0	1.0	1.0	10.0	f	f
	2	2.5	6.0	1.0	2.5	1.0	1.0	1.0	1.0	4.0	s	s
5	3	3.0	5.0	1.0	2.0	0.0	0.0	0.0	0.0	10.0	s	s
	B1	2.0	4.0	1.5	3.5	0.0	0.0	0.0	0.0		s	s
	2	3.0	7.5	1.0	5.5	0.0	1.5	0.0	0.0		f	s
	3	4.5	8.0	1.0	2.5	1.5	0.0	1.5	1.5	10.0	f	s
	A1	5.0	8.5	1.5	3.0	2.0	2.0	0.0	0.0	5.0	f	s
	2	4.0	7.0	1.0	3.0	1.0	0.0	1.0	1.0	—	f	s
6	3	2.0	5.5	1.5	2.0	1.5	1.5	0.5	0.5	6.0	f	f
	B1	1.5	5.0	1.5	5.0	0.0	0.0	0.0	0.0	—	t	t
	2	2.0	6.0	1.0	2.0	1.5	1.5	1.0	1.5	5.0	s	s
	3	4.5	7.5	1.5	2.0	2.5	3.0	1.0	0.0	4.0	f	f
	A1	6.0	9.5	1.5	1.5	0.5	1.0	1.5	1.0	100.0	f	f
	2	4.0	6.0	1.5	2.0	1.5	1.5	0.0	1.0	2.0	t	t
7	3	2.5	5.5	1.5	2.0	1.5	2.0	1.0	0.0	4.0	f	s
	B1	2.0	5.5	1.5	2.0	3.0	3.0	0.0	0.0	8.0	t	s
	2	3.0	6.5	1.0	2.0	2.5	2.5	0.0	1.0	7.0	f	s
	3	5.5	8.0	1.5	3.0	0.3	0.0	0.7	1.0	10.0	t	s
	A1	6.0	7.5	1.5	1.5	1.0	1.0	0.5	0.5	1.0	t	s
	2	3.5	6.0	1.0	3.0	1.0	1.0	0.0	0.0	1.0	s	s
9	3	2.0	5.5	1.0	3.0	1.5	1.5	0.0	0.0	6.0	s	s
	B1	1.5	4.0	1.0	3.0	0.5	0.5	0.0	0.0	1.0	s	s
	2	2.0	6.0	1.5	3.0	2.5	2.5	0.0	0.0	5.0	s	s
	3	6.0	10.0	2.0	2.0	2.5	2.5	1.0	1.0	8.0	t	s
	A1	5.0	7.0	2.0	2.0	1.0	1.0	1.0	1.0	2.0	s	s
	2	3.0	5.5	2.0	2.5	1.0	1.0	1.0	1.0	4.0	t	s
11	3	1.5	3.5	1.0	2.5	0.0	1.0	1.0	0.5	3.0	t	s
	B1	1.5	4.0	1.0	3.0	0.0	0.5	0.5	0.0	5.0	t	s
	2	3.0	5.0	1.5	2.0	0.25	0.5	0.5	0.5	5.0	s	s
	3	4.0	5.5	2.0	2.0	0.5	1.5	1.0	1.0	3.0	s	s

Values for Root, Tip, Zone, and Interzone in terms of millimeters (1 = 3.6 mm.); values for Space in terms of microns (1 = 3.3 μ).

Zone = region of aquatic root hairs.

Interzone = hairless space between amphibious and aquatic root hairs.

Space = approximate average distance between adjacent root hairs on the horizon of the root, in microns.

Curvature = direction of curvature of the root, s, straight, t, affluent, f, effluent.

A = first chamber.
B = second chamber.
o = original length.
l = final length.
t = affluent side of the root.
f = effluent side of the root.

TABLE IV
A SUMMARY OF THE ROOT DEVELOPMENT IN CALCIUM NITRATE

Conc. *M*	pH	Root			Tip			Zone		Interzone		Curv.		
		o	l	d	o	l	d	t	f	t	f	s	t	o
	5.0	4.0	7.6	3.6	1.6	2.1	0.5	3.0		0.0		4	1	1
	6.0	4.3	8.0	3.7	1.6	2.2	0.6	3.0		0.0		4	2	0
	7.0	3.0	7.3	4.3	1.2	2.2	1.0	3.3		0.2		4	1	1
	7.5	4.6	8.7	4.1	1.3	2.0	0.7	3.7		0.0		6	0	0
0.004	8.0	3.4	8.1	4.7	1.2	2.4	1.2	3.5		0.0		6	0	0
	9.0	3.9	7.6	3.7	1.4	2.4	1.0	2.5		0.2		6	0	0
	10.0	4.0	8.8	4.8	1.4	2.2	0.8	3.0		0.2		3	3	0
	11.0	4.0	6.4	2.4	1.5	1.8	0.3	2.0		0.2		1	4	1
	11.5	3.4	4.6	1.2	1.4	3.4	1.0	0.0		—		0	5	1
	4.5	3.6	6.8	3.2	1.4	2.2	0.8	0.8		0.6		4	1	1
	6.0	4.3	8.3	4.0	1.6	2.0	0.4	3.5		0.2		5	0	1
	7.0	4.3	8.1	3.8	1.5	2.1	0.6	3.2		0.3		4	1	1
0.008	8.0	4.5	8.8	4.3	1.5	2.0	0.5	3.5		0.5		4	1	1
	9.0	3.3	7.5	4.2	1.5	2.0	3.0	1.0		0.6		4	2	0
	10.0	4.0	6.6	2.6	1.0	2.0	1.0	2.1		0.6		0	6	0
	10.5	3.6	8.6	5.0	1.1	2.0	0.9	2.0		0.0		0	6	0
	4.0	2.3	4.1	1.8	1.1	2.1	1.0	—		—				
	5.0	3.2	6.4	3.2	1.3	2.4	1.1	2.9	2.9	0.08	0.16	3	1	2
	6.0	4.1	8.6	4.5	1.6	2.1	0.5	3.8	3.8	0.13	0.13	6	0	0
	7.0	4.2	10.4	6.2	1.5	2.4	0.9	4.4	4.6	0.10	0.6	6	0	0
0.012	8.0	3.0	6.2	3.2	1.08	2.1	1.02	2.1	2.2	0.0	0.1	6	0	0
	9.0	4.5	7.6	3.1	1.5	1.9	0.4	1.6	1.2	0.5	0.55	4	2	0
	10.0	3.1	6.6	3.5	1.1	1.8	0.7	2.2		0.2		1	5	0
	10.5	4.4	7.6	3.2	1.5	1.7	0.2	2.7		0.6		0	6	0
	11.0	4.1	6.5	2.4	1.4	1.6	0.2	1.08	0.54	0.5	1.08	3	3	0
	4.5	3.6	7.6	4.0	1.8	3.3	1.5	0.76	0.76	1.1	1.0	5	0	1
	6.0	4.1	7.6	3.5	1.5	2.6	1.1	2.6	2.6	0.3	0.3			
	7.0	3.5	8.3	4.8	0.7	1.6	0.9	3.0	2.8	0.0	0.13	6	0	0
0.020	8.0	4.0	7.8	3.8	1.6	2.2	0.6	3.98	3.13	0.4	0.2	5	0	1
	9.0	3.8	6.5	2.7	1.3	2.08	0.78	1.3	2.2	0.0	0.0	2	2	0
	10.0	3.8	6.8	3.0	1.6	2.1	0.5	2.3	3.0	0.2	0.0	6	0	0
	11.0	3.25	5.6	2.3	1.1	1.0	0.1	0.35	1.1	1.3	0.5	2	0	4
	5.0	3.6	7.6	4.0	1.6	2.5	0.9	0.4	2.0	1.4	1.4	6	0	0
	6.0	2.2	6.4	4.2	1.1	2.8	1.7	2.2	2.2	0.0	0.0	6	0	0
	7.0	3.7	7.4	3.7	2.8	2.7	−0.1	2.6	2.7	0.3	0.4	2	3	1
	8.0	4.1	7.2	3.1	1.2	2.6	1.4	2.0	2.0	0.13	0.1	4	1	1
0.030	9.0	3.5	6.4	2.9	1.3	2.4	1.1	1.3	1.7	0.1	0.15	6	0	0
	9.5	3.6	5.7	2.1	1.0	1.8	0.8	0.8	1.6	3.5	1.5	5	1	0
	10.5	2.6	4.8	2.2	1.1	2.0	0.9	0.6	1.1	0.4	0.3	6	0	0
	11.0	2.6	5.4	2.8	1.1	1.7	0.6	0.2	1.8	1.0	0.3	1	0	5
	11.5	2.6	5.4	2.8	1.3	1.4	0.1	0.0	0.3	0.5	0.5	2	3	1

TABLE IV—*Continued*

Conc. *M*	pH	Root			Tip			Zone		Interzone		Curv.		
		o	l	d	o	l	d	t	f	t	f	s	t	o
	5.0	3.3	6.6	3.3	1.1	3.8	2.7	0.25	0.25	0.58	0.58	5	0	1
	6.0	3.1	6.6	3.5	1.3	2.8	1.5	1.2	1.3	0.58	0.5	3	1	2
0.060	7.0	3.8	6.8	3.0	1.4	2.1	0.7	1.55	1.66	0.53	0.5	4	1	1
	9.0	3.5	6.5	3.0	1.3	2.6	1.3	1.5	1.5	0.25	0.25	6	0	0
	11.0	3.0	5.1	2.0	1.6	2.3	0.7	0.46	0.91	0.83	0.66	0	6	0
	5.0	2.2	3.1	0.9	1.2	1.3	0.1	0.6	0.6	0.5	0.5	5	1	0
0.100	8.0	4.2	5.5	1.3	1.3	1.75	0.45	0.62	2.0	0.50	0.54	5	0	1
	10.5	4.0	5.5	1.5	1.3	1.2	−0.1	0.46	0.54	0.6	0.6	5	1	0
0.120	7.0	3.6	4.6	1.0	1.4	1.3	−0.1	0.8	0.8	0.5	0.3	6	0	0
0.140	7.0	3.5	4.0	0.5	1.0	0.8	−0.2	0.5	0.5	0.3	0.3	6	0	0

Values for Root, Tip, Zone, and Interzone in terms of mm. (1 = 3.6 mm.).
o = original length.
l = final length.
d = l − o.
t = affluent side of the root.
f = effluent side of the root.
s = straight.
o = effluent curvature.
t = affluent curvature.

less region between the portions of the root covered by amphibious hairs and aquatic hairs will not, in every instance, support the author's explanation of the findings in calcium hydroxide (paper VII.) The interzone in these instances was believed to have been produced by an extremely rapid growth of the root, so rapid that the production of root hairs in the horizontal direction was, for a time, suppressed. In calcium nitrate solutions, however, the highest rates of increase in root length do not always correlate with the greatest extent of interzone. The results would indicate that other factors may be involved in this very conspicuous reaction. The findings in calcium nitrate with respect to the interzone would tend to support more strongly the general conclusion in paper V, in which the author explained the presence of the interzone through the temporary suppression of root-hair development, and not as a result of more rapid root elongation.

The assumption that the normal direction of root growth is straight, and that curvatures in either the affluent or the effluent direction represent reactions to toxic conditions, is well substantiated (table IV). In the neutral solutions of lower concentration the six roots, or a large percentage of them, remained straight in most cases. Here again the high concentrations of hydrogen ions seemed to be less toxic than the excessive amounts of hydroxyl ions, a smaller number of roots having shown curvature in the more acid than in the more alkaline solutions. The antagonism of the calcium ion for the hydrogen ion comes out again in solutions of 0.020 *M* and above, the roots showing little or no curvature in the most acid solutions studied in these concentrations.

It may be seen from the data in table IV that interzone formation in 0.012 *M* $Ca(NO)_3$ solutions is more extensive on the effluent side, while in 0.020 *M*, 0.030 *M*, and 0.060 *M* solutions it is more extensive on the affluent side. This reaction would seem to be a response to the degree of acidity or alkalinity of the solutions rather than to their salt concentrations. When the data for interzone formation is presented in terms of salt concentration, this tendency to greater evidence of toxicity upon the affluent side seems to be less conspicuous.

The extent of the zone of root hairs in 0.012 *M* solutions of different H-ion concentrations shows little difference upon the affluent and effluent sides. In 0.020 *M*, 0.030 *M*, and 0.060 *M* solutions, the greater length of zone is found upon the effluent side. These results confirm, in general, the author's earlier suggestion, that in toxic solutions a higher degree of injury was registered upon the affluent side in the form of the presence of an interzone, while a lower degree of toxicity is shown in the more abundant production of root hairs upon the effluent side.

A more general view of the relationship between the concentration of the salt and the various factors presented in table IV may be obtained through a further condensation of this data (table V). Every value here represents the average of the average values obtained in the hydrogen-ion concentrations of the solutions studied. A comparison of these values for root elon-

TABLE V

SUMMARIZATION OF THE DATA GIVEN IN TABLE IV, TO BRING OUT THE EFFECT OF CONCENTRATION OF THE SALT

Conc. *M*	Root length	Tip length	Zone		Interzone		Space
			t	f	t	f	
0.004	3.6	0.8	2.7		0.1		5.8
0.008	7.5	1.0	2.3		0.40		5.9
0.012	3.4	0.67	2.64	2.5	0.26	0.42	5.5
0.020	3.4	0.78	2.04	2.2	0.47	0.30	6.2
0.030	3.09	0.92	1.1	1.7	0.80	0.50	6.8
0.060	2.9	1.4	1.09	1.1	0.5	0.60	4.4
0.10	1.2	0.15	0.56	1.04	0.50	0.50	2.3
0.120	1.0	−0.1	0.80	0.80	0.50	0.30	2.0
0.140	0.50	−0.2	0.50	0.50	0.30	0.30	1.0

gation with those for root-hair elongation in different concentrations of calcium nitrate (fig. 2, paper II), brings out again the tendency to a more delicate reaction by the root hairs than is shown by the root as a whole. The optimum concentration for root elongation, 0.008 *M*, falls near to the optimum for root-hair elongation, 0.012 *M*. The differentiation upon either side of these optima is greater, however, in the root hair than in the root. The data for tip length show that the largest total amount of surface was covered by hairs at a concentration of 0.012 *M*, a point well within the range of solutions which maintained the best conditions for growth of root hairs as well as roots. The values in 0.120 and 0.140 *M* again represent such a limited amount of data that they may be omitted in this comparison. The highest value for the extent of the zone of root hairs occurs at 0.004 *M*, is maintained near to this point in 0.008 *M* and 0.012 *M*, and then declines gradually with a slight increase at 0.120 *M*. The extent of the interzone shows a greater tendency to fluctuate with change in concentration. It is of especial interest to observe the apparent lack of effect of concentration of the salt with respect to unequal growth of root hairs upon the affluent and effluent sides of the root, as shown by the data from the zones and interzones. The values upon the two sides show very little difference, and these differences are not consistent with the findings in solutions of toxic hydrogen- and hydroxyl-ion concentrations reported earlier

by the author. It will be remembered that the greater effect of toxicity in all of the latter type of solutions studied appeared upon the affluent side. The spacing of root hairs is also quite constant in all concentrations which will permit comparison. The values in this connection would undoubtedly be much higher in concentrations from 0.10 *M* to 0.140 *M* if the experiments had covered a range of solution of varying degrees of acidity and alkalinity comparable to that in lower concentrations.

The marked effect of hydrogen-ion concentration of nutrient media upon a wide variety of organisms continues to appear from many sources. Herčik (205) has recently reported a series of experiments upon root elongation in *Pharbitis*, with methods similar to those used in the present study. Weak buffer solutions of primary and secondary sodium phosphate (M/100) were allowed to flow over the roots. To increase the acid N/10 H_2PO_4 was added, and to increase the alkali N/10 tertiary sodium phosphate was added. Electro thermal regulation at 20° C. was maintained in a darkened under-ground room. All of the material for study was prepared in the same place under the same conditions of light, humidity, and temperature. The seedlings were grown in solutions of a definite hydrogen-ion concentration and then transferred suddenly to solutions of differing degrees of acidity. The change in rate of growth was noted every 3 to 5 minutes for 25 minutes. It is interesting to observe the similarity of the curve of permanent growth so obtained to the curve which was shown by the author for collards in a solution of 0.060 *M* calcium chloride, the acid and the alkaline optima, in both instances, falling at 5.8 and 7.6 respectively with the median minimum at 6.2.

Pantin (211), studying the growth of Amoeba in hay infusions ranging in pH values from 5 to 9, found that they thrive best at a pH of 8.2. A bimodal curve was obtained with a median minimum at a pH of 7. Taylor states that amoebae live between pH 3 and pH 8, but thrive best at pH 6.6. Hopkins (206), in a later paper, has given a fuller treatment of the effect of hydrogen-ion concentration upon growth and reproduction in Amoeba. Marked reactions to slight changes in pH were found.

At a pH of 7.2 all were dark and spherical. At a pH of 7.4 nearly all were again normal in appearance, moving about and feeding actively, and at a pH of 7.6 they were larger and more numerous. When the hydrogen-ion concentration had dropped to pH 7.8 the amoebae again became dark and sluggish, but not spherical. Further study of the relation between behavior and hydrogen-ion concentration resulted in a bimodal curve with acid and alkaline optima at pH 6.6 and 8.0–7.6, with a median minimum at about pH 7.1. In explanation of the phenomena the author relies upon the idea of changes in permeability of the membranes due to different hydrogen- and hydroxyl-ion concentrations of the solutions. With the increase in permeability to the salts, an increase in the internal osmotic pressure takes place, and consequently an increase in the water content of the amoeba and a decrease in the rate of locomotion.

Recent studies by Loo (209) on the effect of different pH concentrations upon the growth of seedlings further substantiate the idea of the antagonism of calcium ions for hydrogen ions. His experiments extended over an 8-day period, the seedlings having been introduced into the culture solution when the shoots were 3–9 cms. long. In the presence of calcium ions wheat grew fairly well in a pH of 3 or 4. In the absence of calcium this degree of acidity retarded the growth. Kaho (207), in a study of the roots of legumes, has found that K, Na, NH_3, and Mg injury in a short time begins to kill the roots. The root tip becomes slimy, and the growing zone becomes glassy and transparent. This is accompanied by a cessation in growth of the stem and a drying-up of the heads. The addition of calcium, however, inhibits most of these toxic effects.

A discussion of the necessity for the presence of calcium in connection with the development of many organisms was taken up in an earlier paper of the series (I). It is quite generally believed that its absence leads to the destruction of the cell. It has been considered to be an important component of chloroplasts, nuclei, and membranes in the form of compounds of plastin, nuclein, calcium pectate, callose, etc. Hansteen-Cranner (203), studying the effects of pure salts, found that the cause of toxicity of the salt is not in the structural change of the in-

terior of the cell but in the surface effect. The amount of calcium needed to counteract injurious effects of various salts varies greatly. The quantity needed to overcome the effect of the magnesium ion was far in excess of that needed to antagonize the potassium ion. Sokoloff (201), in a discussion of the dying and super-active (neoplastic) cells to be found in cancer tissue, attributes the rejuvenation in the latter, as shown by their nucleo-plasma ratio, mitochondria, glycogen content, etc., to an alteration of the cellular membrane and cellular lipoids. Nuclear changes, he considers to be secondary in producing the unusual behavior and mentions the possibility that the pathogenic elements may be outside the cell in the lymphoid elements. An interesting study of the relation of calcium to the plasma membrane of eggs of *Arbacea* and *Stentor* has been made recently by Heilbrunn (204). When the eggs were crushed it was observed that, in some instances, films were formed about the extruded cytoplasm, while in others there were no films produced. A series of experiments which followed demonstrated that the film was not due to adsorbed lipoids; that calcium was necessary for the reaction; that magnesium and barium could not be substituted for calcium; that the membrane formed in the absence of calcium is due to the presence of "Ovothrombin"; that the ovothrombin is probably made up of calcium and pigment granules; that the calcium may be in loose combination with a lipoid substance; and that it is freed when the lipoid substance breaks down.

The accumulation of larger amounts of data dealing with simple ionic effects upon various organisms will undoubtedly lead to a clearer understanding of the real nature of the factors concerned in growth. With respect to the rate of root-hair elongation and the other points of interest in root development which have been discussed there has been found to be little difference in the roots of collards grown in calcium nitrate and those grown in calcium hydroxide and chloride. The morphological changes in root hairs have shown greater contrasts in the different salt solutions used and have been treated in a separate paper (VIII).

Moravek (210) has attempted to gain a clearer understanding

of the growth conditions in root hairs by observing the growth of structures formed by the reaction on the boundary between solutions of electrolytes in water and those in a gel. Upon a solidified 0.1 N solution of potassium dichromate in 5 per cent gelatin was placed a layer of 0.1 N solution of lead nitrate. Fibrous structures 0.1 to 0.3 mm. wide grew out into the latter. Their walls were formed by a gelatin membrane with precipitated lead chromate. A stream proceeded through the fiber from the gelatin layer, meeting the lead nitrate solution at the tip of the fiber. A precipitated gelatin layer in the form of a membrane upon which lead chromate is deposited discontinuously grew with a maximal velocity of 0.16 mm. per minute. The chief growth directions are vertical and horizontal. The growth velocity and the dimensions and the shape of the fibers were influenced by the concentration of the gelatin, the addition cf calcium or potassium ions, and the raising of the temperature above 32° C. Light intensity seemed to exert no influence. The cause of the growth in the fiber was attributed to the diffusion stream. This conclusion is entirely in keeping with the findings and interpretations of the author in connection with the diffusion streams in root hairs of collards and discussed in another paper dealing with morphological changes in root hairs of collards on solutions of calcium nitrate (VIII). From observations upon the development of twin hairs, in which the movement of the nucleus into one branch of the hair was accompanied by cessation of growth in that branch, the idea was advanced that the retardation had been caused by the blocking of the diffusion stream by the nucleus.

Conclusions

1. Improvements in the methods of determination of the hydrogen-ion content of the solutions used are described.

2. The curves for the rate of root-hair elongation of collards in dilute solutions of calcium nitrate are shown to be trimodal in contrast to the bimodal curves obtained in calcium chloride.

3. The curves for the rate of root-hair elongation in median concentrations of calcium nitrate are seen to be bimodal, as are those obtained in all except the most concentrated solutions of calcium chloride.

4. The curves for the rate of root-hair elongation in solutions of higher concentrations are monomodal, as were the curves in high concentrations of calcium chloride.

5. The three-dimensional graph from solutions in calcium nitrate shows in dilute solutions, therefore, three optima and two median minima, or perhaps the latter should be called the acid minimum and the alkaline minimum.

6. The median or neutral optimum is shown to be slightly zig-zag. It may be assumed, however, that if the data had been obtained at pH 7.5 instead of at pH 7.0 and 8.0 in the median concentrations that this would have been a straight line also.

7. A floor-plan of the three-dimensional graph for calcium nitrate bears comparable relationships to the limits that were found in calcium chloride.

8. The comparison which may be made by superimposing the one floor-plan upon the other shows that the plant will produce root hairs in a more alkaline solution in nitrate than in chloride.

9. In weak acid solutions nitrate will support root-hair growth better than will chloride.

10. In moderate concentrations root hairs will grow in a more acid solution in chloride than in nitrate.

11. It may be seen that the optima for the two salts bear a definite relation to each other, and that by the shifting of them in the nitrate toward the alkaline side, and the pushing of the acid limit to the lower acid concentrations, room is developed for the insertion of a new acid optimum.

12. The curves obtained for maximum rate of root-hair elongation, for root elongation, and for maximum length of root hairs correspond quite closely to those for average rate of root-hair elongation.

13. In 0.004 *M* solutions root elongation gives a tri-modal curve such as we obtain in root-hair elongation. The locations of the modes do not, however, correspond except in the case of the alkaline optimum.

14. In 0.012 *M* solutions the graphs for the four factors are almost identical, except that the root does not give as good differentiation upon the alkaline side as do the other factors.

15. In solutions of 0.020 *M* there is again a close similarity

in the four graphs. In this instance, however, the acid optimum for the root is at pH 6.0 instead of at pH 8.0 as in the root-hair graphs.

16. In the curves for 0.030 *M* there is a correspondence of root and root-hair activity, but here again the acid optimum for the root is at pH 5.9 instead of at 6.9, as in the root hairs.

17. Curves for 0.060 *M* solutions show a similar correspondence of root and root-hair activity except that, in this case, the acid optimum for the root is at 5.4, instead of at 4.4 for the root hair.

18. It thus appears that there is less variation of the acid optimum with change in concentration of the salt for the root than for the root hair. This may be correlated with the failure of the external solution to impinge its full effect upon the cells on the interior of the root.

19. A summarization of the entire mass of data obtained with reference to the increase in root length, the increase in tip length, the length of the zone of root hairs, the length of the interzone between the amphibious and aquatic hairs, and the spacing of the root hairs is made to bring out the effect of hydrogen-ion concentration in each of the salt concentrations used.

20. A further condensation of this data, so that each concentration at all of the points of acidity and alkalinity will be represented by one value, brings out the effect of salt concentration upon the various factors.

21. We have by this method a means of comparing different chemical ions as to their biological effect on a more or less accurate mathematical basis.

22. It is believed also that the method presents an accurate method of study of the specific effect of different substances upon a simple cell process, namely, cell enlargement.

Bibliography[1]

203. Hansteen-Cranner, B. ('14). Über das Verhalten der Kulturpflanzen zu den Bodensalzen, III. Beiträge zur Biochemie und Physiologie der Zellwand lebender Zellen. Jahrb. f. wiss. Bot. **53**: 536–599. *pl. 5–7. f. 1–5.* 1914.

[1] The references in this series of papers are numbered consecutively from paper No. I.

204. Heilbrunn, L. V. ('27). The colloid chemistry of protoplasm. V. A preliminary study of the surface precipitation reaction of living cells. Archiv f. exp. Zellforsch. **4**: 246–263. 1927.

205. Hercik, F. ('25). On the growing reactions produced by the change of hydrogen-ion concentration in germinating roots of Pharbitis hispida Choisy. Univ. Masaryk, Publ. Fac. Sci. 49: 3–20. *f. 1–7.* 1925.

206. Hopkins, D. L. ('26). The effect of hydrogen-ion concentration on the locomotion and other life processes in Amoeba proteus. Nat. Acad. Sci., Proc. **12**: 311–315. *f. 1.* 1926.

207. Kaho, H. ('26). Das Verhalten der Pflanzenzelle gegen Salze. Ergebn. d. Biol. **1**: 380–406. 1926.

208. Kisser, J. ('25). Über das Verhalten von Wurzeln im feuchter Luft. Jahrb. f. wiss. Bot. **64**: 416–439. *f. 1–2.* 1925.

209. Loo, T. ('27). The influence of hydrogen-ion concentration on the growth of the seedlings of some cultivated plants. Bot. Mag. Tokyo **41**: 33–41. 1927.

210. Moravek, V. ('25). On the growth of structures formed by reactions on the boundary between solutions of electrolytes in water and those in gel. Univ. Masaryk, Publ. Fac. Sci. 59: 3–42. *pl. 1–5.* 1925.

211. Pantin, C. F. A. ('23). On the physiology of amoeboid movement. Marine Biol. Assoc. United Kingdom, Jour. N. S. **13**: 24–68. *f. 1–10.* 1923.

212. Turner, T. W. ('26). The effect of varying the nitrogen supply on the ratios between the tops and roots in flax. Soil Sci. **21**: 303–306. 1926.

HYSTERANGIUM IN NORTH AMERICA[1]

SANFORD M. ZELLER

Plant Pathologist, Oregon Agricultural College and Experiment Station
Formerly Visiting Fellow in the Henry Shaw School of Botany of Washington University

AND CARROLL W. DODGE

Curator of the Farlow Herbarium, Harvard University
Formerly Rufus J. Lackland Fellow in the Henry Shaw School of Botany of Washington University

HYSTERANGIUM

Hysterangium Vittadini, Monogr. Tuberac. 13–15. 1831; Tulasne, Fung. Hypog. 80–85. 1851; Winter in Rabenhorst, Krypt.-Fl. Deutschl. ed. 2, I. **1**: 878–879. 1883; DeToni in Sacc. Syll. Fung. **7**: 155–158. 1888; Hesse, Hypog. Deutschl. **1**: 94–105. 1891; Harkness, Cal. Acad. Sci. Proc. III. **1**: 254–257. 1899; E. Fischer in Engl. & Prantl, Die Nat. Pflanzenfam. I. **1****: 306. 1899; Bucholtz, Материалы къ морфологiи и систематикѣ подземныхъ грибовъ (Tuberaceae И Gastromycetes pr. p.) съ приложенiемъ описанiя видовъ, найденныхъ до сихъ поръ въ предѣлахъ Россiи. Издан. Естеств. Ист. Музея Графини Е. П. Шереметевой въ с. Михайловскомъ Московской Губ. **1**: 151–153. 1902 [sometimes cited as Beitr. Morph. Syst. Hypog.]; Th. M. Fries, Svensk Bot. Tidskr. **3**: 279–281. 1909; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911**: 26–27. 1912; Soehner, Pilz und Krauterfreund **5**: 254–256. 1922.

Hyperrhiza Endlicher, Gen. Pl. 28. 1836 (in part).

Splanchnomyces Corda, Icones Fung. **6**: 37–45. 1854 (in part).

The type species of the genus is considered to be *Hysterangium clathroides* Vittadini in accordance with the recommendations of the Committee on Nomenclature of the Botanical Society of America, Bot. Soc. Am. Publ. 73: 70–71. 1919, since the author states that he has collected this species many times and describes it at greater length.

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Fructifications spherical, ellipsoidal, oblately spheroidal to reniform and irregular; fibrils filiform, terete or flattened, loose to innately appressed, simple or anastomosing, usually less prominent than in *Rhizopogon*, leading to rhizomorphs, usually dark-colored; peridium simple or duplex, of fibrous, parenchymatous or pseudoparenchymatous context, usually separable, indehiscent; gleba lacunose, usually tough, gelatinous-cartilaginous, penetrated from the basal attachment by a simple or dendroid columella of fibrous or pseudoparenchymatous tissue; septa fibrous or pseudoparenchymatous, often radiating from columella; basidia 1–several-spored; spores smooth (sometimes with loose epispore), typically fusiform to elongate-ellipsoidal, sometimes ovoidal, greenish, brownish or white in mass.

Hysterangium is so familiar to mycologists, and its relationships have been so fully treated by one of us[1] that its characteristics need not be discussed here. In 1831 Vittadini included in the genus hypogaeous Gasteromycetes having smooth spores and peridia which dissolve or split off at maturity. Since then the genus has been emended to include species with semi-persistent or indehiscent peridia, but its limits are characteristic and for the most part unmistakable. Cunningham's[2] genus, *Phallobata*, is closely related to *Hysterangium* through *Hysterangium Phillipsii* Harkness.

This paper describes 31 species and lists 2 doubtful and 3 excluded species. Sixteen are European, 19 North American, 4 South American, 2 African, and 7 from Australia or near-by islands. Within the United States the species are found principally along the Pacific Coast where in California and Oregon alone 15 species are reported. Three species have been found in New England, two in New York, three in Tennessee, two in North Carolina, and one each in Ohio and Wyoming.

There are 5 named varieties described. Among the 31 species, there is one newly named, 11 are here first described in Latin, of which 7 are described as new by the writers, and one new combination is proposed.

[1] Dodge, C. W. Gasteromycetes in Gäumann & Dodge, Comparative morphology of Fungi, p. 492 et seq. New York, 1928.

[2] Cunningham, G. H. A new genus of the Hysterangiaceae. New Zealand Inst. Trans. **56**: 71–73. 1926.

We have followed the plan, adopted in previous taxonomic papers, of giving the data and location of specimens cited. Unless otherwise stated, colors have been compared with Ridgway's 'Color Standards and Color Nomenclature,' Washington, D. C., 1912.

We gratefully acknowledge those who have made this work possible by putting at our disposal personal collections or the facilities of libraries and herbaria. We are indebted to the Missouri Botanical Garden for the use of its library and herbarium; to Leland Stanford Jr. University for access to the Dudley Herbarium, and to Dr. LeRoy Abrams and Professor J. McMurphy for assistance in the study of Harkness' specimens there; to Dr. P. Claussen of Marburg University for a loan of Hesse's material; to Dr. J. B. Cleland for Australian collections; to Dr. G. H. Cunningham for New Zealand material; to Harvard University for access to collections at the Farlow Herbarium, and to Dr. R. Thaxter for putting at our disposal many of his own collections, and for helpful suggestions; to the late Mr. C. G. Lloyd for the courtesies of the Lloyd Museum; to Mr. H. E. Parks for many of his collections and notes on freshly collected material; to Mr. L. Rodway for Tasmanian collections; to Drs. W. A. Setchell and N. L. Gardner for access to the herbarium of the University of California; and to Dr. Ert Soehner for authentic material of *H. Rickeni.*

Key to the Species of Hysterangium

1. Peridium wholly or in part parenchymatous or pseudoparenchymatous 2
1. Peridium without parenchyma or pseudoparenchyma 16
    2. Gleba purplish brown (dry) . . . . *H. purpureum* (p. 110)
    2. Gleba brownish, yellowish or ochraceous (dry) 3
    2. Gleba greenish (dry) 7
3. Peridium in one layer of pseudoparenchyma 4
3. Peridium in more or less distinct layers 5
    4. Peridium membranous, 400 μ or more thick . . . . *H. stoloniferum* and variety (p. 111, 112)
    4. Peridium compact, 120–320 μ thick . . . . *H. neocaledonicum* (p. 113)
    4. Peridium of larger, softer-walled cells, 90–110 μ thick . . . . *H. album* (p. 87)
5. Both layers of peridium pseudoparenchymatous . . . . . . *H. neglectum* (p. 88)
5. One layer of the peridium filamentous and one layer parenchymatous 6
    6. Peridium 350–640 μ thick; fructifications large, 3–6 cm. in diameter; septa about 200 μ thick . . . . *H. occidentale* (p. 89)
    6. Peridium 240–320 μ thick; fructifications less than 2 cm. in diameter; septa 50–80 μ thick . . . . *H. strobilus* (p. 90)

7. Peridium of a single layer 8
7. Peridium of more than one layer 13
  8. Spores mostly 5 μ or less in length . . . . . *H. Phillipsii* (p. 91)
  8. Spores 7 μ or more in length 9
9. Septa more than 70 μ thick 10
9. Septa less than 60 μ thick 12
  10. Peridium separated from gleba by a definite filamentous layer 11
  10. Peridium not separated from the gleba by a definite filamentous layer; septa 70–150 μ thick; peridium 120–240 μ thick . . . . . *H. affine* and varieties (p. 92, 93)
11. Septa less than 175 μ thick; peridium 220–450 μ thick . . . *H. clathroides* (p. 93)
11. Septa more than 220 μ thick; peridium 100–200 μ thick . . . . . *H. clathroides* var. *crassum* (p. 96)
  12. Septa 12–30 μ thick; spores 7–10 μ long; peridium 320–375 μ thick . . . . . *H. obtusum* (p. 97)
  12. Septa 45–60 μ thick; spores 12–17 μ long; peridium 65–160 μ thick . . . . . *H. inflatum* (p. 98)
13. Peridium more than 200 μ thick 14
13. Peridium less than 200 μ thick 15
13. Peridium 100–240 μ thick, outer layer cottony-filamentous, inner pseudoparenchymatous; spores 13–18 μ long . . . . . *H. nephriticum* (p. 99)
  14. Outer peridial layer definitely parenchymatous, 80–200 μ thick, inner layer pseudoparenchymatous; spores 8–12μ long . . *H. coriaceum* (p. 113)
  14. Both peridial layers parenchymatous, outer layer about 25 μ thick; spores 13–22 μ long . . . . . *H. crassirhachis* (p. 101)
15. Outer peridial layer pseudoparenchymatous, inner filamentous . . . . . *H. siculum* (p. 114)
15. Outer peridial layer filamentous, inner pseudoparenchymatous . . . . . *H. Harknessii* (p. 102)
  16. Peridium of more than one layer 17
  16. Peridium of one layer 18
17. Spores less than 6 μ long; peridium more than 1500 μ thick . . . . . *H. Thaxteri* (p. 114)
17. Spores more than 10 μ long; peridium less than 500 μ thick . . . . . *H. cinereum* (p. 103)
  18. Peridium less than 60 μ thick 19
  18. Peridium more than 70 μ thick 20
19. Septa 10–15 μ thick; spores 7.5–11 × 5–6 μ . . . . . *H. membranaceum* (p. 104)
19. Septa 25–60 μ thick; spores 14–15 × 4–5 μ . . . . . *H. pumilum* (p. 115)
  20. Gleba buff, brownish, yellowish or ochraceous 21
  20. Gleba greenish 24
21. Spores less than 17 μ long; peridium mostly more than 180 μ thick 22
21. Spores 17–21 × 6–8 μ; peridium 160–180 μ thick; fructifications drying wood-brown . . . . . *H. Thwaitesii* (p. 116)
  22. Spores 12 μ or more long and broadly fusiform 23
  22. Spores 12 μ or less long and narrowly fusiform; fructifications drying buckthorn-brown to mummy-brown . . . . . *H. fuscum* (p. 105)
23. Fructifications drying ochraceous buff to russet; spores light buff in mass; gleba drying fragile . . . . . *H. rubricatum* (p. 105)

23. Fructifications drying buffy olive to light brownish olive; spores olivaceous in mass; gleba drying hard................*H. Pompholyx* (p. 106)
   24. Peridium less than 300 μ thick..................................25
   24. Peridium more than 400 μ thick..................................26
25. Spores fusiform, 10–17 × 6–7.5 μ; septa 50–120 μ thick..*H. cistophilum* (p. 107)
25. Spores fusiform, sometimes papillate, 15–18 × 6–7 μ.....*H. Rickeni* (p. 117)
25. Spores ellipsoid, 8–11 × 4–5.5 μ; septa 35–80 μ thick.....*H. Fischeri* (p. 109)
   26. Spores more than 17 μ long; peridium more than 1000 μ thick...... ....*H. fragile* (p. 118)
   26. Spores less than 15 μ long; peridium less than 700 μ thick............27
27. Peridium 600 μ thick, of alternate layers of light and dark brown hyphae. ....*H. calcareum* (p. 119)
27. Peridium 500 μ thick, homogeneous, yellow-spotted........*H. Petri* (p. 119)

1. Hysterangium album Zeller & Dodge, sp. nov.

Pl. 1, fig. 1; pl. 3, fig. 5.

Fructificationes globosae vel depressae, ad 7 mm. diametro metientes, "cartridge-buff" (Ridgway); columella dendroidea, tenuis; peridium separabile, 90–110 μ crassitudine, pseudoparenchymate hyalino, hyphis superficialibus, crystallis oxalatis incrustatis; gleba "cartridge-buff" (Ridgway) vel obscuratior; locelli magni, vacui, globosi vel irregulares; septa hyalina, 50–150 μ crassitudine, hyphis compacte contextis; basidia clavata vel ovata, ad 13 × 7–8 μ, bispora, rarius tetraspora, sterigmatibus brevibus; sporae hyalinae vel cremeae acervatae, fusiformes, papillatae, appendiculatae, 13–21.5 × 5–7 μ.

Type: in Fitzpatrick Herb., in Dodge Herb., and in Zeller Herb.

Fructifications spherical or somewhat depressed-globose, up to 7 mm. in diameter, cartridge-buff when dry; columella dendroid, small; peridium separable, 90–110 μ thick, pseudoparenchymatous, with superficial hyphae which are encrusted with oxalate crystals; gleba cartridge-buff or darker, consisting of a few large cavities in older specimens; cavities empty, rounded to irregular; septa hyaline, 50–150 μ, composed of compactly interwoven hyphae; basidia small, hyaline, clavate to ovate, 13 × 7–8 μ, usually 2-spored, rarely 4-spored; sterigmata short; spores hyaline, cream-colored in mass, smooth, broadly fusiform, usually with a papillate apex and base with short appendage, 13–21.5 × 5–7 μ.

This species seems to have close affinities with *H. neocaledonicum* Patouillard, but it differs in general color, size, and texture, and in the thickness of the peridium which is of a looser texture than in *H. neocaledonicum*.

Specimens examined:

New York: Ithaca, *H. M. Fitzpatrick, 364*, type (in Fitzpatrick Herb., Dodge Herb., and in Zeller Herb. 2800).

2. Hysterangium neglectum Massee & Rodway, Kew Bull. Misc. Inf. **1899:** 181. 1899; Saccardo & P. Sydow in Sacc. Syll. Fung. **16:** 247. 1902; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911:** 27. 1912; **1923:** 156. 1924. Pl. 3, figs. 2, 7.

Type: probably in Kew Herb. and in Rodway Herb.; cotype in Dodge Herb. and Zeller Herb.

Fructifications 1–1.5 cm. in diameter, drying to less than 1 cm., rugulose, white when fresh, drying clay color to Saccardo's umber; mycelium not seen; columella large, penetrating to the middle of the fructification, much-branched, branches penetrating to peridium; fibrils prominent, waxy, concolorous or darker; peridium 160–250 μ, not separable, duplex, the outer layer up to 80 μ, very variable in thickness, deep brown under the microscope, pseudoparenchyma of narrow, thick-walled cells; the inner layer 80–170 μ, composed of hyaline, thin-walled pseudoparenchyma, most of whose cells are periclinal; gleba subgelatinous, drying Prout's brown to bister, cavities elongate, 160–200 μ in diameter, nearly filled with spores at maturity; septa hyaline, 30–40 μ between hymenia, composed of very slender hyphae with gelatinized walls; basidia 7 × 9 μ, hyaline, oblong-pyriform with four slender sterigmata 4–5 μ long; spores smooth, broadly ellipsoid to ovoid, 14–18 × 7–8 μ, brownish, epispore thick, spores more or less stuck together by the gelatinization of walls, usually long-pedicellate.

Under *Quercus*. Oregon and Tasmania. October.

Because of the shape and color of the spores this species has about as close affinities with *Hymenogaster* as *H. inflatum* has with *Dendrogaster*.

Specimens examined:

Oregon: Linn Co., *S. M. Zeller* (in Oregon Agr. Coll. Herb. 4866, and Zeller Herb. 2583).

Tasmania: Hobart, *L. Rodway 614*, cotype (ex Massee Herb. in N. Y. Bot. Gard. Herb.); *1118* (in Lloyd Mus.); *1263, 1266* (in Dodge Herb. 337, 349, in Zeller Herb. 7224, 7225).

3. Hysterangium occidentale Harkness, Cal. Acad. Sci. Proc. III. **1**: 255. 1899; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 245. 1902. Pl. 3, figs. 1, 9.

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications spherical to somewhat depressed, 3 × 6 × 6 cm., of firm consistency from abundant rhizomorphic growth in soil, dirty white to pallid mouse-gray, darkening to drab or hair-brown in alcohol, fibrils few, concolorous, conspicuous, free to adnate; base not prominent; columella penetrating at least to the middle of the fructification, branched, with a cartilaginous appearance when fresh; peridium duplex, separable, 350–640 μ thick; outer layer often flaking off, 85–300 μ thick, dark brown, composed of brown hyphae in rhizomorph-like periclinal strands, loosely interwoven, clamp-connections frequent; inner layer parenchymatous, 260–400 μ thick, parenchyma not compact, characterized by long hypha-like cells, as in illustration (pl. 3, fig. 1); gleba light pink when fresh (Parks), becoming buckthorn-brown to raw umber in alcohol or when dry; cavities empty, radiating from columella; septa 200 μ thick, composed of closely woven, gelatinized hyaline hyphae; basidia linear, filiform, collapsing, 2–4-spored; sterigmata short, stout; spores yellow-brown in mass, ellipsoidal, cell wall thickened at apex, 12–16 × 5–7 μ.

Under *Quercus*. Oregon and California. Spring and early summer.

Mature plants are nearly odorless or have the pleasant odor of some species of *Polyporus*. Fruiting bodies are tough and rubbery when fresh. It is a large coarse species.

Specimens examined:

Oregon: Benton County, Corvallis, *S. M. Zeller, 7063* (in Oregon Agr. Coll. Herb. 4868, and Zeller Herb. 7063).

California: Marin County, Mt. Tamalpais, *H. W. Harkness, 242*, cotype (in Dudley Herb. at Leland Stanford Jr. Univ.); Santa Clara County, Alma, *H. E. Parks, Z26* (in Zeller Herb. 1712, and Univ. Cal. Herb. 468); Morgan Hill, *C. W. Dodge & M. S. Clemens* (in Dodge Herb. 1533 and 1534).

4. Hysterangium strobilus Zeller & Dodge, sp. nov.
Pl. 1, fig. 6; pl. 3, fig. 11.

Fructificationes subsolitariae, globosae, 1–1.5 cm. diametro metientes, siccatae minus quam 1 cm., argillaceae servatae, subalbidae siccatae; columella magna, arborea, velut strobili *Pini Strobi*, percurrens, basis rhizomorphis confecta, funiculis alteris destitutis; peridium 240–320 μ crassitudine, tenuibus hyphis 2–3 μ diametro dense compactum, hyphis exteris superficiei perpendicularibus, intus 65–120 μ, parenchymate hyalina; gleba elastica, cacaotica brunnea recens, olivacea siccata; locelli irregulares, sporis subimpleti; septa subscissilia, 50–80 μ crassitudine, magnis hyalinis hyphis gelatinosis; basidia cylindrica (an collapsa?) bi- vel tetra-spora, 12–16 × 3–6 μ; sterigmata 5–12 × 2–2.5 μ; sporae 12–16.5 × 5–6.3 μ, subfusiformes.

In fagetis, Tennessee.

Type: in Thaxter Herb.

Fructifications subsolitary, globose, 1–1.5 cm. in diameter, drying less than 1 cm., clay color in alcohol, nearly white when dry; columella large, dendroid, resembling the cones of *Pinus Strobus* when seen in section, percurrent; base of rhizomorphs but no other fibrils; peridium duplex, 240–320 μ thick, outer layer 120–250 μ, composed of slender, loosely woven hyphae 2–3 μ in diameter, with some hyphae often running perpendicular to the surface, somewhat in strands, inner layer 65–120 μ, of hyaline parenchyma, easily separable from gleba; outer layer separable from inner layer of peridium; gleba rubbery in consistency, chocolate-brown when fresh, drying olive; cavities irregular, partially filled with spores; septa somewhat scissile, 50–80 μ thick, composed of large hyaline hyphae with gelatinous walls; basidia cylindrical (or collapsed?) 2–4-spored, 12–16 × 3–6 μ; sterigmata stout, 5–12 × 2–2.5 μ; spores 12–16.5 × 5–6.3 μ, brown, subfusiform, with heavy exospore, which is rather loosely sheathing in dry specimens.

Under *Fagus*. Tennessee.

This species is most closely related to *H. occidentale* Harkn. in structure of peridium and color and texture of gleba, but it is smaller in the dimensions of all of the sterile tissues. *H. occidentale* is a larger, coarser species. *H. strobilus* is similar to *H. Harknessii* in peridial characters but differs in color and texture of the gleba.

Specimens examined:

Tennessee: Burbank, *R. Thaxter*, *B4H*, type (in Thaxter Herb.).

5. Hysterangium Phillipsii Harkness, Cal. Acad. Sci. Proc. III. **1**: 255. 1899; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 216. 1902. Pl. 3, fig. 26.

Illustrations: Harkness, Cal. Acad. Sci. Proc. III. **1**: *pl. 42, f. 1.*

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications 3–6 cm. in diameter, ellipsoid to pyriform in shape, rose-pink (Harkness), Mars brown to warm sepia in alcohol, fibrils none; base rhizoidal-branching, very long; columella penetrating to middle of fructification, branching; peridium about 275 μ thick, of thin-walled cells which are olivaceous brown, 3–4 μ, forming a collapsed pseudoparenchyma? underlaid with a thick layer (about 400 μ) of white sterile gelatinous glebal tissue; gleba deep olive to jade-green; septa 40 μ between hymenia, hyaline; basidia, 2–2.5 × 7–9 μ, cylindric, 2-spored; sterigmata filiform, 3–4 μ; spores oblong, appendiculate, hyaline to olivaceous, 3–5 × 1–1.5 μ.

In coniferous and hard wood forests. Ohio and Pacific Coast. Spring and summer.

This species is more nearly a radicate or stipitate species than any of this genus. The basal portion, however, is a contraction of the peridium which leads to a dense mass of mycelium of white or pale pink strands. The surface of the fruiting bodies is subnitid-glabrous with small shallow pits lighter in tint than the surrounding surface. The Ohio collection was taken from the surface of a very rotten, continually wet log, where the fructifications were entirely superficial.

Cunningham's new genus, *Phallobata*,[1] surely has its closest relationship to the genus *Hysterangium*, through *H. Phillipsii*. *Phallobata* is found on decaying wood, as was the large collection of Ohio material of *H. Phillipsii*. Both are distinctly radicate and have similar spores.

Specimens examined:

Ohio: Herrouns Woods, Maumee Valley near Toledo, *W. R. Lowater, No. ORAN* (in Dodge Herb. 2847, Oregon Agr. Coll. Herb. 4869, and Zeller Herb. 7227).

[1] Cunningham, G. H. A new genus of the Hysterangiaceae. New Zealand Inst. Trans. **56**: 71–73. 1926.

Oregon: Corvallis, *W. H. Dreesen* (in Zeller Herb. 1849, and Dodge Herb. 356).

California: Placer County, Wire Bridge, *C. L. Phillips* (H. W. Harkness, 234, cotype, in Dudley Herb. at Leland Stanford Jr. Univ.).

6. **Hysterangium affine** Massee & Rodway, Kew Bull. Misc. Inf. **1898**: 127. 1898; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 246. 1902; Rodway, Roy Soc. Tasmania Papers & Proc. **1911**: 27. 1912; **1923**: 154–155. 1924. Pl. 2, fig. 1; pl. 3, fig. 6.

Type: in Kew Herb. and in Rodway Herb. but not seen.

Fructifications 1–2 cm. in diameter, white at first, drying pinkish buff to avellaneous; mycelium white, terete, branched; fibrils scarce, black, innate, small, only on the under side of the fructification; columella dendroid; peridium easily separable, 120–240 μ thick, composed of parenchyma of large, thin-walled cells, the outer layer of sterile glebal tissue 200–220 μ thick, composed of thick-walled, hyaline, highly gelatinized hyphae 3–4 μ in diameter, often so regular as to make the peridium appear duplex; gleba "toughly gelatinous, dark greenish slate" (Rodway), the freshly cut gleba deep slate-olive to dull greenish black (1), but the fractured surface, after drying, is gnaphalium-green to sage-green, very hard; cavities irregular, small, filled with spores; septa 70–150 μ thick, composed of highly gelatinized hyphae 5–7 μ in diameter; basidia clavate, 4–6-spored, 16–18 × 6 μ; sterigmata short; spores hyaline, ellipsoidal, 8–15 × 3–5.5 μ (average 9.7 ± 0.4 μ).

Under *Quercus* and *Eucalyptus*. Oregon and Tasmania. June to October.

Specimens examined:

Oregon: Linn County, *S. M. Zeller, 2585* (in Oregon Agr. Coll. Herb. 4855, and Zeller Herb.).

California: Alameda County, Shepard Canon, near Oakland, *H. E. Parks, 1168, 1169* and *C. W. Dodge* (in Univ. Cal. Herb., Zeller Herb., and Dodge Herb. 1582, 1580).

Tasmania: Hobart, Cascades, *L. Rodway, 1122*, and unnumbered specimen (in Lloyd Mus. 1122 and 086); Proctor's Road, *L. Rodway, 1261* (in Dodge Herb. 308, and Zeller Herb. 7064).

Australia: South Australia, Mt. Lofty, *J. B. Cleland, 8* (in Cleland Herb., Dodge Herb. 2848, and Zeller Herb.).

6a. Var. **irregulare** Massee, Kew Bull. Misc. Inf. **1901**: 158. 1901; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911**: 27. 1912.

Hysterangium Eucalyptorum Lloyd, Myc. Notes **65**: 1031. 1921; **66**: 1119–1120. 1922.

Illustrations: Lloyd, Myc. Notes **66**: *f. 2132.*

Type: probably in Kew Herb. and Rodway Herb. but not seen.

This variety was distinguished by its irregular outlines, by its thinner peridium, darker gleba, and smaller spores, but the extreme variations in size of the spores of a single fructification are greater than those given for this variety.

On roots of *Eucalyptus.* Ecuador and Tasmania.

Specimens examined:

Ecuador: Quito, *L. Mille, 3*, type of *H. Eucalyptorum* (in Lloyd Mus.).

6b. Var. **tenuispora** Rodway, Roy. Soc. Tasmania Papers & Proc. **1911**: 27. 1912.

Type: probably in Rodway Herb. but not seen.

This variety was distinguished from the type by the thinner peridium, nearly black gleba, and slender spores 12–14 × 2.5–3 μ in length, being more than four times the width instead of less than three times as in the species.

7. Hysterangium clathroides Vittadini, Monogr. Tuberac. 13–14. 1831; Corda, Anleit. z. Stud. Myc. 110. 1842; Icones Fung. **5**: 26. 1842; Tulasne, Fung. Hypog. 80–82. 1851; DeToni in Sacc. Syll. Fung. **7**: 155–156. 1888; Hesse, Fung. Hypog. **1**: 98–100. 1891; Harkness, Cal. Acad. Sci. Proc. III. **1**: 256. 1899; Bucholtz, Материалы къ морфологiи и систематикѣ подземныхъ грибовъ . . . Издан. Естеств. Ист. Музея Графини Е. П. Шереметевой въ С. Михайловскомъ Московской губ. **1**: 152–153. 1902 [often cited as Beitr. Morph. Syst. Hypog.]; Th. M. Fries, Svensk Bot. Tidskr. **3**: 280. 1909; Rodway, Roy.

Soc. Tasmania Papers & Proc. **1911**: 27. 1912; 1923; 155–156. 1924; Th. C. E. Fries, Arkiv f. Bot. **17**⁹: 18. 1921.

Pl. 2, fig. 3; pl. 3, fig. 12.

Splanchnomyces clathroides Corda (ed. Zobel), Icones Fung. **6**: 41. 1854.

Hysterangium stoloniferum var. *americanum* Fitzpatrick, Ann. Myc. **11**: 129–135. 1913.

Rhizopogon virens Fries, Syst. Myc. **2**: 294. 1823 (excl. syn. sec. spec. in Herb. Fries, fide Th. M. Fries, Svensk Bot. Tidskr. **3**: 280. 1909); Karsten, Finska Vet.-Soc. Bidrag Natur och Folk **25**: 354–355. 1876 [Myc. Fenn. **3**: 354–355. 1876]; *Ibid.* **48**: 18–19. 1889 [Krit. Ofversigt af Finl. Basidsv. 18–19. 1889]. —*Rhizopogon virescens* Karsten in Sacc. Syll. Fung. **9**: 280. 1891 (sec. spec. in Herb. Karsten, fide Th. M. Fries, Svensk Bot. Tidskr. **3**: 280. 1909).

Illustrations: Vittadini, Monogr. Tuberac. *pl. 4, f. 2;* Corda, Anleit. z. Stud. Myc. *pl. D, f.* 46^{1-4}; Icones Fung. **6**: *pl. 8, f. 77;* Hesse, Hypog. Deutschl. **1**: *pl. 1, f. 10–14; pl. 7, f. 19;* E. Fischer, in Engl. & Prantl, Die Nat. Pflanzenfam. I. **1**: 305. *f. 154;* Gillet, Champ. Fr. Gast. **3**: *pl. 28;* Bucholtz, *l. c. pl. 1, f. 16;* Fitzpatrick, Ann. Myc. **11**: *f. 2, 6, 10, 20–28.*

Type: location unknown to us.

Fructifications globose, becoming very irregular on drying, white to pale ochraceous buff or light ochraceous salmon when fresh, becoming buff-pink to onion-skin pink where bruised, drying ochraceous tawny to Prout's brown; fibrils variable from terete and free to innate or appressed; columella usually large and prominent, often branching near the base; peridium 220–450 μ thick, parenchymatous, the cells varying from 12 to 40 μ in diameter (see pl. 2, fig. 3); gleba green when fresh, becoming citrine drab or grayish olive to dark greenish olive on drying; cavities polyhedral to irregular, with a tendency to radiate from the columella, small, empty; septa 85–140 μ thick, composed of large, thin-walled, loosely woven hyphae up to 5–7 μ in diameter, finally becoming highly gelatinized; basidia long, irregularly cylindrical, 3–4-spored (mostly 3-spored); sterigmata usually short, although sometimes becoming 16–18 μ long; spores acrogenous, olivaceous in mass, lanceolate, 12–19 × 6–8 μ (averaging

15.3 ± 0.9 μ long), with a thick epispore which sometimes is slightly roughened and becomes loosened in age, sometimes papillate at apex, sometimes not.

Under oaks and other deciduous trees. Cosmopolitan.

This species has a white peridium which turns brown or rusty on exposure to the air. The more or less brittle peridium is easily separable. The gleba is tough and gristly when fresh. The plants are usually found scattered or densely crowded in rocky soil or in soil-filled pockets on rocky ledges. The taste of young plants is pleasant, but the odor of mature ones is so offensive that tasting would be difficult. Hollós, who studied an authentic specimen from Vittadini communicated by Mattirolo, states that the spores are 14–18 × 6–7 μ.

Specimens examined:

Exsiccati: L. Fuckel, Fungi Rhenani Suppl. 2616; Transhel & Serebrianikov, Mycoth. Ross. 216.

Russia: Moscow, Mikhailovskoe, *F. Bucholtz* in Transhel & Serebrianikov, Mycoth. Ross. 216 (in Farlow Herb.).

Czechoslovakia: Cechy, Vloi dul ad Tabor, *F. Bubak* (in von Hoehnel Herb. at Farlow Herb. and in Lloyd Mus. 05861).

Austria: Wiener Wald, *F. von Hoehnel* (in von Hoehnel Herb. at Farlow Herb.); also specimen of *G. Bresadola* det. *H. Thwaitesii* without locality (in Patouillard Herb. at Farlow Herb.).

Germany: Altmorschen, *R. Hesse* (in Farlow Herb.).

Maine: Kittery, Gerrish Island, *R. Thaxter* (in Thaxter Herb.).

Vermont: Rutland County, Pawlet, *C. W. Dodge* (in Dodge Herb.).

New York: Ithaca, Coy Glen, *F. M. Blodgett* (in N. Y. State Coll. Agr. Cornell Univ. Plant Path. Herb. 5342, in Zeller Herb., Lloyd Mus., and Dodge Herb.); *H. H. Whetzel* (in N. Y. State Coll. Agr. Cornell Univ. Plant Path. Herb. 8269, Zeller Herb., and Dodge Herb.); *H. M. Fitzpatrick*, type of *Hysterangium stoloniferum* Tul. var. *americanum* Fitzp. (in N. Y. State Coll. Agr. Cornell Univ. Plant Path. Herb. 8448, Zeller Herb., and Dodge Herb.).

Wyoming: Medicine Bow National Forest, *C. H. Kauffman & B. B. Kanouse* (in Univ. Mich. Crypt. Herb., and in Zeller Herb. 7049).

Oregon: Corvallis, *L. M. Boozer, 35, 36* (in Oregon Agr. Coll. Herb. 4871, 4872, Zeller Herb. 2209, 2801, and Dodge Herb. 320, 321); *S. M. Zeller, 2074, 2582, 7191* (in Zeller Herb., Oregon Agr. Coll. Herb. 4857, 4858, and Dodge Herb.).

California: Placer County, Auburn, *H. W. Harkness, 140* (in Dudley Herb. at Leland Stanford Jr. Univ.); Marin County, Mill Valley, *H. W. Harkness, 119* (in Dudley Herb. at Leland Stanford Jr. Univ.); San Rafael, *H. E. Parks, 2043, 2096, 2111* (in Univ. Cal. Herb. and Zeller Herb.); Santa Clara County, Aldercroft Creek, *H. E. Parks, 60* (in Dodge Herb. 311, and Zeller Herb. 7196), *Z327* (in Zeller Herb. 1662); Saratoga, *H. E. Parks, 452, 971, 978, 992, 995, Z21* (in Univ. Cal. Herb., Zeller Herb. 1664, 7207, 7208, 7210, 7211, 1686, and Dodge Herb. 315, 313, 314, 316, 317); Guadaloupe, *H. E. Parks, 315, 326, 347, 363, 382, 383, 869, Z16* (in Univ. Cal. Herb., Zeller Herb. 1652, 7205, 1718, 7209, 7206, 1674, 7202, 1699, and Dodge Herb. 324, 322, 323, 325, 326, 1508); Alma, *H. E. Parks, 78, 406, 491* (in Univ. Cal. Herb., Zeller Herb. 1657, 7212, 7204, and Dodge Herb. 328, 330); Call of the Wild, *H. E. Parks, 943c* (in Univ. Cal. Herb., Zeller Herb. 7213, and Dodge Herb. 327); Santa Cruz County, Felton, *H. E. Parks, 505* (in Univ. Cal. Herb., Zeller Herb. 7214, and Dodge Herb. 329); Brookdale, *H. E. Parks, 2163* (in Univ. Cal. Herb.).

Chile: Magellanes, Punta Arenas, *R. Thaxter* (in Thaxter Herb.).

7a. Var. **crassum** Tulasne, Fung. Hypog. 81–82. 1851.

Hysterangium clathroides Fuckel, Jahrb. Nassau Ver. f. Naturk. **27**: 11. 1873 [Symb. Myc. Nachtr. **2**: 11. 1873]; Winter in Rabenhorst, Krypt.-Fl. Deutschl. ed. 2, I. **1**: 879. 1883; ? Coker & Couch, Gast. E. U. S. & Can., 17–18. 1928, non Vitt.—*Not* Fuckel, Jahrb. Nassau. Ver. f. Naturk. **23**: 38. 1869 [Symb. Myc. 38. 1869].

Type: a portion ex herb. Tulasne in Patouillard Herb. at Farlow Herb.

The variety is distinguished by its larger size, thin, white, smooth peridium, easily separable even in young specimens, covered with a loose, cottony mycelium; gleba glaucous-virescent,

becoming greenish ashy and even clay-color; septa very much thicker than in the type, dark green to almost black. The odor is very pungent, becoming fetid at maturity.

Specimens examined:

Exsiccati: L. Fuckel, Fungi Rhenani Suppl. 2509.

Germany: Altmorschen, *R. Hesse* (in Farlow Herb.).

Switzerland: Chur, *L. Fuckel*, in Fungi Rhenani Suppl. 2509 (in Farlow Herb.).

France: Paris, Parc de Maisons, *L. R. Tulasne*, type (in Patouillard Herb. at Farlow Herb.).

Maine: Kittery, *R. Thaxter, 1902a* (in Thaxter Herb.).

Oregon: Corvallis, *S. M. Zeller, 2581, 7058* (in Oregon Agr. Coll. Herb. 4859, 4864, and Zeller Herb.).

California: *H. E. Parks, 561, 1131* (in Univ. Cal. Herb., Zeller Herb. 7216, and Dodge Herb. 333); Santa Clara County, Guadaloupe, *H. E. Parks, 949, 998* (in Univ. Cal. Herb., Zeller Herb. 7215, 7217, and Dodge Herb. 1502, 2849); Alma, *H. E. Parks, Z28* (in Univ. Cal. Herb., Zeller Herb. 1709, and Dodge Herb. 332); Aldercroft Creek, *H. E. Parks, 38, 1154,* and *Dodge, 1523* (in Zeller Herb. 1658, 2718, and Dodge Herb.); Eva, *H. E. Parks, C. W. Dodge & S. M. Zeller* (in Zeller Herb. 2118, and Dodge Herb. 2850).

8. Hysterangium obtusum Rodway, n. sp. Pl. 3, figs. 3, 10.

Hysterangium obtusum Rodway, Roy. Soc. Tasmania Papers & Proc. **1919**: 112. 1920; **1923**: 156. 1924 (English description only).

Type: in Rodway Herb., cotype in Dodge Herb. and Zeller Herb.

Fructificationes sphaeroideae, irregulares, 2 cm. diametro metientes, siccatae 1.5 cm. minusve, "pale pink-violet" (Rodway) recens lectae, "light pinkish cinnamon to Sayal brown" (Ridgway) siccatae; mycelium non visum; columella fruticosa; funiculi non visi; peridium crassum 320–375 μ, hyphis tenuibus dense compactum, hyphis exteris brunneo-violaceis; gleba "pale slatey olive" (Ridgway) recens, "dark greenish olive" (Ridgway) siccata; locelli parvi, irregulares, partim sporis impleti; septa 12–30 μ, hyphis tenuibus gelatinosis dense compactis; basidia 17–20 × 5–6 μ, hyalina, cylindrica, sterigmatibus brevibus; sporae ellipsoideae, 7–10 × 4–5 μ, subbrunneae, leves, epispora crassa.

Fructifications spheroidal, irregular, 2 cm. in diameter, drying to 1.5 cm. in diameter or less, pale pink-violet, drying light

pinkish cinnamon to Sayal brown; mycelium not seen; columella branching at the base and penetrating to the center of the fructification as in *Jaczewskia;* fibrils not seen; peridium 320–375 μ thick, composed of spongy pseudoparenchyma, the outer portion of which is tinged brownish violaceous; gleba "pale slatey olive," drying dark greenish olive; cavities small, irregular, partially filled with spores; septa 12–30 μ thick (when distended after drying), composed of slender gelatinous hyphae closely woven; rhaches of the columella same as septa, but 25–50 μ thick; basidia 17–20 × 5–6 μ, hyaline, cylindric; sterigmata short; spores broadly ellipsoidal to obovoidal, 7–10 × 4–5 μ, slightly brownish, smooth with a rather thick epispore.

Specimens examined:

Exsiccati: Torrend, Mycoth. Lusitan. 90, under *Hysterangium clathroides* var.

Portugal: Mafra, *C. Torrend,* in Mycoth. Lusitan. 90 (in Farlow Herb.).

California: Marin County, Mt. Tamalpais, *H. E. Parks, 3049* (in Univ. Cal. Herb.).

Tasmania: Mt. Nelson, *L. Rodway, 1264,* cotype (in Dodge Herb. 354, and Zeller Herb. 7228).

9. Hysterangium inflatum Rodway, sp. nov.

Pl. 2, fig. 4; pl. 3, fig. 19.

Hysterangium inflatum Rodway, Roy. Soc. Tasmania Papers & Proc. **1917:** 108. 1918; **1923:** 156. 1924 (English description only).

Fructificationes subglobosae, circa 1 cm. diametro, quae siccatae induresсunt, cinnamoneo-rufae vel castaneae; peridium 65–160 μ crassitudine, subhyalinum sectum superficie brunnea, parenchymate, separabile; gleba dura siccata, "dark grayish blue-green" vel "greenish slate-black" (Ridgway) septis albidis, gelatinosa recens; locelli subglobosi, 240 μ diametro vel amplius, sporis impleti; septa 45–60 μ crassitudine, hyalina, hyphis magnis hyalinis 5–7 μ diametro metientibus contextis; basidia truncato-clavata, 18–22 × 7–9 μ, sterigmatibus brevibus, 3- vel 7-spora; sporae fusiformes, olivaceo-alutaceae acervatae, hyalinae sub lente, 12–17 × 5–7.5 μ, subappendiculatae, epispora inflata laevi, 14–18 × 10–11 μ metiente, spora longiore sed apice depresso.

Type: in Rodway Herb., cotype in Dodge Herb. and Zeller Herb.

Fructifications subglobose, about 1 cm. in diameter, becoming

very hard when dry, cinnamon-rufous to chestnut-brown; peridium 65–160 μ thick, light brown in section except the darker brown surface composed of parenchyma, separating from the gleba; gleba hard when dry, dark grayish blue-green to greenish slate-black, veined with whitish septa, very gelatinous when fresh; cavities subglobose, 240 μ or larger, filled with spores; septa 45–60 μ thick, hyaline, composed of large longitudinal hyphae 5–7 μ in diameter; basidia truncate-clavate, hyaline, 18–22 × 7–9 μ, with short sterigmata, 3–7-spored; spores fusiform, deep olive-buff in mass to almost hyaline singly under the microscope, 12–17 × 5–7.5 μ, slightly appendiculate, surrounded by a hyaline, smooth, inflated membrane measuring 14–18 × 10–11 μ, somewhat attenuated below, exceeding the spore below but depressed at the apex, exposing the tip of the spore.

California, New Zealand, and Tasmania.

Hysterangium inflatum has closer affinities to the genus *Dendrogaster* than do other species of *Hysterangium*. The inflated exospore is characteristic of *Dendrogaster* but in all other respects *H. inflatum* is like *Hysterangium*.

In young material, part of cotype, the spores are first without the inflated sheath. Some spores show only a shriveling of the outer wall, perhaps the beginning of sheath production.

Specimens examined:

California: Santa Clara County, Aldercroft, *H. E. Parks, 2026* (in Univ. Cal. Herb.).

Tasmania: Mt. Wellington, *L. Rodway, 1267*, cotype (in Dodge Herb. 342, and Zeller Herb. 7223).

New Zealand: Auckland, TeAroha, *G. H. Cunningham, 1189* (in Cunningham Herb.).

10. Hysterangium nephriticum Berkeley, Ann. & Mag. Nat. Hist. **13**: 350. 1844; Outlines Brit. Fungol. 294. 1860; Tulasne, Fung. Hypog. 82. 1851; Cooke, Handb. Brit. Fung. **1**: 358. 1870; De Toni in Sacc. Syll. Fung. **7**: 156. 1888; Hesse, Hypog. Deutschl. **1**: 104–105. 1891. Pl. 3, fig. 16.

Splanchnomyces nephriticum Corda, Icones Fung. **6**: 79. 1854.

Illustrations: Berkeley, Birmingham Nat. Hist. Soc. Rept. &

Trans. **1881:** *pl. 3, f. 10;* Corda, Icones Fung. **6:** *pl. 8, f. 79;* Hesse, Hypog. Deutschl. **1:** *pl. 7, f. 2, 5;* Massee, Ann. Bot. **4:** *pl. 1, f. 4* [Monogr. Brit. Gast. *pl. 1, f. 4*]; Brit. Fung. Fl. **1:** 11. *f. 4;* Smith, Brit. Basid. 490. *f. 143.*

Type: in Berkeley Herb. at Kew; fragment ex herb. Tulasne in Patouillard Herb. at Farlow Herb.

Fructifications 2–2.5 cm. in diameter, drying to less than 1 cm., white at first, drying clay-color or lighter; mycelium white, flat, branched, membranous; columella scarcely more than a sterile base with several branches, as in *Jaczewskia;* fibrils large, prominent and flaky at point of attachment; peridium duplex, 100–240 μ thick, easily separating, especially on drying, as the gleba contracts much more than the peridium, cartridge-buff in cross-section; outer part of first layer cottony, loosely woven, of hyaline, thick-walled hyphae about 6–7 μ in diameter, and inner part of parallel smaller hyphae, and the second layer of pseudoparenchyma about 40 μ thick; gleba at first cartilagineo-glutinous, "pale blue or gray in parts with a green tinge or even pinkish" in very young specimens, drying clay-color and fragile, with columella becoming Kaiser brown on drying; cavities small, nearly filled with spores; septa 85–120 μ thick, composed of loosely interwoven, hyaline hyphae 2–3 μ in diameter, with a tendency to become scissile; basidia cylindric, 2–3 × 17–18 μ long, hyaline, sterigmata short; spores ellipsoidal, 13–18 × 4–6 μ, slightly brownish, more or less stuck together by a gel.

Under *Quercus.* Europe and North America. September to February.

Fructifications of this species are found imbedded in a mass of white mycelial strands which are attached to them at several points. The gleba is first pinkish, then greenish, often drying clay color. The odor is not offensive.

Specimens examined:

England: near Bristol, *C. E. Broome 2/45* (J. W. Bailey Herb. 305, in Brown Univ. Herb.); *C. E. Broome* (in Curtis Herb. at Farlow Herb. and ex-Massee Herb. in N. Y. Bot. Gard. Herb.); near Clifton, *C. E. Broome,* type (in Patouillard Herb. at Farlow Herb.).

Maine: Kittery Point, *R. Thaxter* (in Farlow Herb.).

California: Marin County, Rattlesnake Camp, *H. E. Parks, 2174* (in Univ. Cal. Herb.); Santa Clara County, Guadaloupe, *H. E. Parks, 149, 385* (in Univ. Cal. Herb., Dodge Herb. 351, 352, and Zeller Herb. 7226, 1677).

11. Hysterangium crassirhachis Zeller & Dodge, sp. nov.

Pl. 1, fig. 4; pl. 3, fig. 20.

Fructificationes reniformes, albae dein "sea-shell pink" (Ridgway) vel carneae recens lectae, "pinkish buff" vel "snuff-brown" (Ridgway) siccatae; stipes 1–2 mm. diametro, albus, semper peridio albior siccatus, stuposus, subparallelibus vel anastomosantibus, hyalinis, hyphis 2–2.5 μ diametro compactus, cum capite in medio fructificationis crassissimo (⅓ diametro fructificationis metiente) ex quo radiant lamellae 300–450 μ crassitudine, tenaces, hyphis gelatinosis hyalinis contextis; peridium facile separabile, 400–500 μ crassitudine, pseudoparenchymate, cellulis 8–17 μ diametro strato extero cellulis brunneis 25 μ diametro; gleba gelatinosa recens "grayish olive" vel "deep grayish olive" (Ridgway); locelli simplices vel labyrinthiformes, vacui; septa 85–100, vel etiam 200 μ crassitudine, hyphis gelatinosis hyalinis contexta; basidia di- vel tetraspora, 30–50 × 6–9 μ, hyalinis; sterigmata brevia; sporae fusiformes leves, episporis crassis, uni- vel multiguttulatae breve appendiculatae hyalinae vel olivaceae acervatae, 13–22 × 4–8 μ.

In quercetis et aceretis. Oregon et California. Primo vere.

Type: in Zeller Herb., Dodge Herb., and Oregon Agr. Coll. Herb.

Fructifications spheroidal to depressed, often reniform, 1–2.5 cm. in diameter, white at first, becoming sea-shell pink to flesh-colored when fresh, drying pinkish buff to snuff-brown; stipe in a depression at the base, 1–2 mm. in diameter, white, drying somewhat lighter than the rest of the fructification, stupose, composed of more or less parallel and anastomosing, slender, hyaline hyphae 2–2.5 μ in diameter; columella neutral gray to slate-gray, opalescent when fresh, drying white, flinty, thick, terminating in a broad head at the center of the fructification, covering about one-third of the median vertical section, whence radiate distinct, percurrent branches which are usually at least 300–450 μ thick, tough, composed of highly gelatinized, hyaline, interwoven hyphae; peridium easily separable, 400–500 μ thick, duplex, inner and major portion parenchymatous, composed of hyaline rhomboidal cells, 8–17 μ in diameter, with an outer rind of smaller, thin pseudoparenchyma of brownish cells about 25 μ thick; gleba gelatinous, from grayish olive to deep grayish

olive when fresh; cavities radiating from the columella to the peridium, sometimes simple, appearing as linear openings in sections, but usually labyrinthiform, broken by septa jutting out from the columellar branches on either side, not filled; septa from 85–100 up to 200 μ broad, of interwoven, hyaline hyphae, highly gelatinized; basidia 2–4-spored, 30–50 × 6–9 μ, hyaline; sterigmata short; spores fusiform, smooth, thick-walled, sometimes 1–many-guttulate, hyaline to olivaceous in mass, 13–22 × 4–8 μ, short-appendiculate.

Under *Quercus* and *Acer*. Oregon and California. May.

These plants are characterized by the brittle peridium, which is easily separable when fresh, and by the tough, rubbery gleba with its large translucent septa which become flinty when dry.

Specimens examined:

Oregon: Benton County, Corvallis, *L. M. Boozer*, type (in Zeller Herb. 2319, Dodge Herb. 334, and Oregon Agr. Coll. Herb. 4862); *L. M. Boozer* (in Zeller Herb. 2320); Sulphur Springs, *Helen M. Gilkey* (in Oregon Agr. Coll. Herb. 4861, 4860, and Zeller Herb. 2343, 2348).

California: Marin County, San Rafael, *H. E. Parks, 3037* (in Univ. Cal. Herb.); Santa Clara County, Alma, *H. E. Parks, 156* (in Dodge Herb. 338, Zeller Herb. 7219, and Univ. Cal. Herb.); Mt. Umunhum, *H. E. Parks, 897* (in Univ. Cal. Herb., Dodge Herb. 340, and Zeller Herb. 7220); Saratoga, *H. E. Parks, 815, 2160* (in Dodge Herb. 339, 2851, and in Univ. Cal. Herb.).

12. Hysterangium Harknessii Zeller & Dodge, sp. nov.

Pl. 3, fig. 24.

Hysterangium australe Harkness, Cal. Acad. Sci. Proc. III. **1**: 256. 1899, *not H. australe* Spegazzini, Soc. Cientif. Arg. Anal. **11**: 242–243. 1881 [often cited as Fung. Arg. **4**: 94. 1881].

Type: in Dudley Herb. at Leland Stanford Jr. Univ.

Fructificationes ellipsoideae, 1 × 1 × 1.5 cm. metientes, argillaceae vel fulvae; columella tenuior; peridium tenue, 90–135 μ crassitudine, intus tenuibus hyphis 3–4 μ diametro minusve, hyphis exteris superficiei fructificationis perpendicularibus; gleba viridis, locellis luteis, subimpletis; septa 120–300 μ crassitudine, hyphis magnis laxe implexis, gelatinosis; basidia non visa; sporae 13–18 × 5–6 μ, fusiformes, subappendiculatae, luteae.

In quercetis. California.

Type: in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications ellipsoidal, 1 × 1 × 1.5 cm., clay-color to tawny; columella branching, slender; peridium thin, 90–135 μ thick, composed of thick-walled hyphae 3–4 μ in diameter, duplex, the inner portion compact, pseudoparenchymatous, cells mostly periclinal, 40–50 μ, the outer 50–85 μ, composed of loosely interwoven radial hyphae; gleba dark green, with yellowish cavities, nearly filled; septa 120–300 μ thick, composed of large, thin-walled, loosely interwoven, gelatinizing hyphae; basidia not seen; spores 13–18 × 4–6 μ, fusiform, slightly appendiculate, yellowish.

Under *Quercus*. California. April.

Harkness referred four specimens to *Hysterangium australe* Spegazzini, of which Nos. 119 and 140 are *H. clathroides*, No. 155 is *Hysterangium* sp., and No. 84, the only specimen mentioned by number by Harkness (*l. c.*), is taken as the *type* of *H. Harknessii.* The outer layer of the peridium is almost identical with that of *H. strobilus*, but the inner layer is pseudoparenchymatous while in *H. strobilus* it is parenchymatous. These two species also differ in dimensions of sterile tissues and in color and texture of the gleba.

Specimens examined:

California: Marin County, Mt. Tamalpais, *H. W. Harkness, 84*, type (in Dudley Herb. at Leland Stanford Jr. Univ.).

13. **Hysterangium cinereum** Harkness, Cal. Acad. Sci. Proc. III. **1**: 254. 1899; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 245. 1902.

Illustrations: Harkness, Cal. Acad. Sci. Proc. III. **1**: *pl. 42, f. 2.*

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructifications depressed-globose, 1 × 2 cm., cinnamon to bister in alcohol; fibrils scanty, small, concolorous, base not prominent; columella large at base, branching; peridium duplex, 300 μ thick, outer layer of dark brown hyphae 4–5 μ in diameter, inner layer of gelatinized hyphae 3–8 μ in diameter, compact; gleba firm, dark olive-buff to citrine-drab; cavities empty; septa 80–90 μ thick, of compact, gelatinized hyphae; basidia cylindric, 10–14 × 4–5 μ; sterigmata 11–12 μ long; spores greenish yellow, rhomboid-ellipsoidal to allantoid, 12–16 × 4–7 μ.

Under *Arctostaphylos* and *Quercus*. California. February to June.

Specimens examined:

California: Placer County, Auburn, *H. W. Harkness, 31*, cotype (in Dudley Herb. at Leland Stanford Jr. Univ.); Marin County, Mt. Tamalpais, *H. E. Parks, 3050* (in Univ. Cal. Herb.); San Rafael, *H. E. Parks, 2043* (in Univ. Cal. Herb.); San Mateo County, Redwood Park, *H. E. Parks, 2190* (in Univ. Cal. Herb.); Santa Clara County, Aldercroft Creek; *H. E. Parks, 1153*, and *C. W. Dodge* (in Dodge Herb. 1522); Saratoga, *H. E. Parks, 1155*, and *C. W. Dodge* (in Dodge Herb. 1524).

14. Hysterangium membranaceum Vittadini, Monogr. Tuberac. 14. 1831; Tulasne, Fung. Hypog. 83. 1851; Winter in Rabenhorst, Krypt. Fl. Deutschl. ed. 2, I. **1**: 879. 1883; DeToni in Sacc. Syll. Fung. **7**: 156. 1888; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911**: 26. 1912; **1923**: 157. 1924. Pl. 3, fig. 17.

Splanchnomyces membranaceus Corda, Icones Fung. **6**: 41. 1854.

Illustrations: Vittadini, Monogr. Tuberac. *pl. 4, f. 15;* Corda, Icones Fung. **6**: *pl. 8, f. 78;* Patouillard, Tab. Anal. *f. 364*.

Type: location unknown to us.

Fructifications nearly spherical, 0.8–1 cm. in diameter, cream-color when fresh, drying tilleul-buff to wood-brown; columella short and inconspicuous, not extending more than half way to the center of the fructification; peridium thin, membranous, papery, separable, 25–55 μ thick, composed of parallel, thin-walled, brownish hyphae; gleba court-gray when fresh, becoming warm buff when dry; cavities minute and irregular; septa very thin, 10–15 μ, sometimes scissile; basidia narrow-cylindrical, 2–3-spored; spores almost hyaline, about 7.5–11 × 5–6 μ, ovate to ellipsoidal.

Under *Acer*. Cosmopolitan. July in Tasmania, October in Oregon.

Specimens are tiny and quite ill-scented, like musty wine.

Specimens examined:

Oregon: Linn County, *S. M. Zeller, 2584* (in Oregon Agr. Coll. Herb. 4865, and Zeller Herb.).

Tasmania: Hobart, *L. Rodway* (in Lloyd Mus. 083); Cascades, *L. Rodway, 1270* (in Dodge Herb. 345, and Zeller Herb. 7224); Waterworks, *L. Rodway, 1120* (in Lloyd Mus.).

15. Hysterangium fuscum Harkness, Cal. Acad. Sci. Proc. III. **1:** 257. 1899; Saccardo & P. Sydow in Sacc. Syll. Fung. **16:** 247. 1902. Pl. 3, figs. 4, 14.

Hysterangium Gardneri E. Fischer in Fedde, Rep. Nov. Sp. **7:** 194. 1909; Saccardo & Trotter in Sacc. Syll. Fung. **21:** 495. 1912.—*H. Gardneri* E. Fischer, Ber. d. deut. bot. Ges. **25:** 276. 1907 (nom. nud.); Bot. Zeit. **66:** 164–166. 1908.

Illustrations: E. Fischer, Bot. Zeit. **66:** *pl. 6, f. 19.*

Type: cotype in Dudley Herb. at Leland Stanford Jr. Univ.

Fructification spherical, 1–2 cm. in diameter, buckthorn-brown to mummy-brown and clover-brown in alcohol; fibrils scarce, not prominent although becoming nearly free below, innate-appressed above, concolorous, hence inconspicuous; columella percurrent or nearly so, slender, not conspicuously branched; peridium 200–235 μ thick, of coarse, thick-walled, closely interwoven, dark brown hyphae; gleba isabella color to olive-brown; septa 45–75 μ thick, of fine gelatinized hyphae; basidia ellipsoidal with short sterigmata; spores yellow-brown, fusiform, 10–12 × 4–5 μ.

Under *Eucalyptus*. California. March.

Specimens examined:

California: Marin County, Mill Valley, *H. W. Harkness, 177,* cotype (in Dudley Herb. at Leland Stanford Jr. Univ.); Alameda Co., Shepard Canon near Oakland, *H. E. Parks, 1167, 1172,* and *C. W. Dodge, 1586, 1589* (in Univ. Cal. Herb., Dodge Herb., and Zeller Herb. 7189); Berkeley, *N. L. Gardner,* type of *H. Gardneri* (in Univ. Cal. Herb. 214).

16. Hysterangium rubricatum Hesse, Jahrb. f. wiss. Bot. **15:** 631. 1884; Hypog. Deutschl. **1:** 95–97. 1891; DeToni in Sacc. Syll. Fung. **7:** 491. 1888. Pl. 3, fig. 27.

Illustrations: Hesse, Jahrb. f. wiss. Bot. **15:** *pl. 32;* Hypog. Deutschl. **1:** *pl. 1, f. 1–5; pl. 5, f. 13, 14; pl. 6, f. 1, 9, 10.*

Type: not seen, but authentic material from Hesse in Farlow Herb.

Fructifications variable in size, 1–4 cm. in diameter, spherical to reniform; columella usually drying to slender, branched, dendroid veins, from a slight thickening at the base; peridium 150–400 μ thick, at first white, drying light ochraceous buff to russet, the outer portion very compact, with abundant crystals of calcium oxalate, the inner layers composed of more loosely woven hyphae, with clamp-connections and studded with oxalate crystals; gleba pale purplish to light pink when fresh (Parks), drying fragile, usually pinkish buff to Sayal brown; cavities labyrinthiform, small; septa hyaline, 25–100 μ thick, composed of compact, parallel hyphae; basidia mostly 2-spored, hyaline, 16–18 × 6–7 μ; sterigmata short; spores broadly fusiform, granular, hyaline to light buff in mass, appendiculate, smooth, 12–17 × 5–8 μ.

Under *Quercus*, *Arbutus*, and *Fagus*. Pacific Coast of North America and Germany. Spring.

Large groups of fruiting bodies are often found on one mycelium. They are first white, becoming reddish brown on exposure to the air.

Specimens examined:

Germany: *R. Hesse* (in Farlow Herb., also ex Mattirolo, 19, in Lloyd Mus.).

Oregon: Corvallis, *S. M. Zeller, 7193* (in Oregon Agr. Coll. Herb. 4870, and Zeller Herb.).

California: Marin County, San Rafael, *H. E. Parks, 2109, 2123* (in Univ. Cal. Herb.); Santa Clara County, Alma, *H. E. Parks, 157, 468* (in Univ. Cal. Herb., in Dodge Herb. 363, 364, and in Zeller Herb. 1680, 7230), and Guadaloupe Mines, *H. E. Parks, 141, 386, 413, 861, 959* (in Univ. Cal. Herb., in Dodge Herb. 360, 361, 359, 1500, 358, and in Zeller Herb. 1676, 1693, 7195, and 7194); Saratoga, *H. E. Parks, Z20, Z23, 451* (in Zeller Herb. 1684, 1687, 7231).

17. Hysterangium Pompholyx Tulasne, Ann. Sci. Nat. Bot. II. **19**: 375. 1843; Fung. Hypog. 83–84. 1851; DeToni in Sacc. Syll. Fung. **7**: 157. 1888; ? Coker & Couch, Gast. E. U. S. & Can., 19–20. 1928. Pl. 3, fig. 23.

Illustrations: Tulasne, Ann. Sci. Nat. Bot. II. **19**: *pl. 17, f. 17–19;* Fung. Hypog. *pl. 2, f. 3; pl. 11, f. 6.*

Type: fragment from Tulasne Herb. in Patouillard Herb. at Farlow Herb.

Fructification at first white, becoming reddish and then dark brown, 1–1.5 cm. in diameter, globose to depressed-globose, surface with flakes of white mycelium or flocculent with more or less fascicled hyphae; columella extending three-fourths the length of the fructification, branched; peridium 300–600 μ thick, composed of septate hyphae more or less braided together, variable in size, with enlarged, irregular cells, darker brown toward the surface, hyaline within, the open canals in the peridium being about 20–22 μ in diameter; gleba at first white, then dull reddish brown, drying buffy olive to light brownish olive, compact; cavities radially arranged; septa 90–120 μ thick, composed of parallel, compact, hyaline hyphae; basidia large, cylindric, 35–40 × 7–8 μ; spores dilute olivaceous in mass, 12–14 × 5–6 μ, short elliptic-fusiform, apices usually rounded, sometimes with a slightly roughened exospore.

Under *Carpinus* and *Fagus*. France and eastern North America.

Specimens examined:

France: Aisne, Foret de Marly, *N. Patouillard* (in Patouillard Herb. at Farlow Herb.); Seine et Oise [? Meudon], *L. R. Tulasne*, type (fragment in Patouillard Herb. at Farlow Herb.).

Maine: Kittery Point, *R. Thaxter*, "6 Je '86" (in Thaxter Herb.).

Tennessee: Burbank, *R. Thaxter* (in Thaxter Herb. B3H).

18. Hysterangium cistophilum (Tulasne) Zeller & Dodge, sp. nov. Pl. 2, fig. 2; pl. 3, fig. 22.

Hysterangium clathroides Tulasne in Durieu de Maison-Neuve, Expl. Sci. de l'Algérie, Bot. **1**: 395. 1846–1849.—*H. clathroides* Vittadini var. *cistophilum* Tulasne, Fung. Hypog. 81. 1851; Bataille, Soc. Myc. France Bull. **39**: 168. 1923.

Illustrations: Durieu de Maison-Neuve, Expl. Sci. de l'Algérie, Bot. **1**: *pl. 24, f. 7–11.*

Type: R. Maire, Mycoth. Bor.-Afric. **13**: 311.

Fructifications spherical to reniform, 1–2.5 cm. in diameter, at first white, becoming red-brown on exposure, drying pinkish buff to tawny olive, growing from ramose, white rhizomorphs;

columella not well developed but, when apparent, dendroid with thin branches; peridium tough, 70–170 μ thick, scarcely separable in young specimens to easily separable at maturity, loosely to closely stupose, composed of brownish hyphae, mostly parallel to the surface; gleba dark green (Parks) or deep olive (Tulasne and Thaxter) when fresh, becoming buffy citrine to olive-citrine when dry; cavities small but long and narrow, mostly arranged radially with reference to their longest diameter, empty; septa 50–120 μ thick, hyaline, composed of compact, parallel hyphae, somewhat gelatinized; basidia obovate to clavate, 2–4-spored, 10–18 × 5–6 μ, sterigmata short; spores almost sessile, fusiform, yellowish to dilute olivaceous under the microscope, slightly appendaged, smooth, 10–17 × 6–7.5 μ (average 13.1 ± 0.7 × 6.5 μ). Odor similar to that of ether (Tulasne).

Gregarious or singly under a thin layer of leaves. Under *Quercus*, *Arbutus*, *Eucalyptus*, and *Pistacia*. Cosmopolitan.

A fragment ex herb. Tulasne, without locality, in the Patouillard Herb. at the Farlow Herb. agrees with the above in all respects.

Specimens examined:

Exsiccati: R. Maire, Mycoth. Bor.-Afric. **13**: 311, under the name *Hysterangium clathroides* Vitt. var. *cistophilum* Tul.; Migula, Cryptog. Germ. Austr. et Helv. Exsicc. 191, under the name *Hysterangium clathroides* Vitt.

Austria: Wiener Wald, *F. von Hoehnel* (in von Hoehnel Herb. at Farlow Herb.).

Czechoslovakia: Cechy, *F. Bubak*, in Migula, Cryptog. Germ. Austr. et Helv. Exsicc. 191, under the name *Hysterangium clathroides* Vitt. (in Farlow Herb. at Harvard Univ.).

Germany: Eisenkaute, *R. Hesse* (Herb. Bot. Inst. Univ. Marburg).

Algeria: Baali prés Souma, *A. Duvernoy & R. Maire*, type, in R. Maire, Mycoth. Bor.-Afric. **13**: 311, under the name *Hysterangium clathroides* Vitt. var. *cistophilum* Tul. (in Farlow Herb. at Harvard Univ.).

Oregon: Benton County, Corvallis, *S. M. Zeller, 7197* (in Oregon Agr. Coll. Herb. 4856, and Zeller Herb.).

California: Santa Clara County, Saratoga, *H. E. Parks, 292*,

980 (in Dodge Herb. 2127, 2128, and in Zeller Herb. 7198); Guadaloupe, *H. E. Parks, 148* (in Dodge Herb. 2130, and Zeller Herb. 7201).

Chile: Punta Arenas, *R. Thaxter*, two collections (in Thaxter Herb.).

19. Hysterangium Fischeri Zeller & Dodge, sp. nov.

Pl. 1, fig. 2; pl. 3, fig. 8.

Hysterangium sp. (near *H. siculum*) E. Fischer, Ber. d. deut. bot. Ges. **25**: 375–376. 1907.—*Hysterangium* Nr. 258, E. Fischer, Bot. Zeit. **66**: 163–164. 1908.

Type: in Univ. Cal. Herb.

Fructificationes irregulares, depresso-globosae, 2–3.5 × 1–2 cm. metientes, "Natal brown" servatae, "avellaneous" vel "wood-brown" siccatae; columella basi ramosa, tenuis; peridium 90–200 μ crassitudine, stuposum, hyphis magnis, granulosis, flavobrunneis, 5–8 μ diametro, extus laxe implexis, intus tenuioribus compacte contextis; gleba "buffy citrine" vel "olive citrine"; locelli parvi, irregulares, sporis impleti; septa 35–80 μ crassitudine, hyphis tenuibus, 3–5 μ diametro contexta, gelatinosa; basidia 2–5-spora, 10–12.6 × 2.5–5.5 μ; sporae "old gold," ellipsoideae, basi truncatae, laeves, 8–11 × 4–5.5 μ.

Fructifications irregularly depressed-globose, 2–3.5 × 1–2 cm., Natal brown, drying avellaneous to wood-brown; columella branching almost at the base of the fructification, slender, inconspicuous; peridium 90–200 μ thick, stupose, composed of granulose, large, thin-walled, yellow-brown hyphae 5–8 μ in diameter, loosely woven toward the outside, slightly smaller and more compactly woven within; gleba buffy citrine to olive-citrine; cavities very small, irregular, filled with spores; septa 35–80 μ thick, composed of slender, thin-walled hyphae 3–5 μ in diameter, becoming highly gelatinized at maturity; basidia obscure, 2–5-spored, 10–12.6 × 2.5–5.5 μ; spores acrogenous, old-gold, ellipsoidal, often truncate at the base, smooth, 8–11 × 4–5.5 μ. No odor.

Under *Quercus* and *Eucalyptus*. Oregon, California, and Australia. February to May.

Specimens examined:

Oregon: Corvallis, *S. M. Zeller, 7056* (in Oregon Agr. Coll. Herb. 4863, and Zeller Herb.).

California: Alameda County, Berkeley, *W. A. Setchell & C. C. Dobie*, type (in Univ. Cal. Herb. 258); Oakland, *C. W. Dodge &*

H. E. Parks, 1166 (in Dodge Herb. 1579, and Zeller Herb. 7221); San Mateo County, Redwood Park, *H. E. Parks & Martha Watson, 13* (in Univ. Cal. Herb. 2229); Santa Clara County, Alma, *H. E. Parks, 997* (in Univ. Cal. Herb.).

Australia: Victoria, *F. Martin, 467* (in Kew Herb.).

EXTRA-LIMITAL SPECIES

1. **Hysterangium purpureum** Zeller & Dodge, sp. nov.
Pl. 1, fig. 5; pl. 3, fig. 21.

Fructificationes ad 2 cm. metientes, laete lavendulicoloris, purpurascentes tactu, siccatae "grayish olive" vel "citrine drab" (Ridgway), "dull purplish black" (Ridgway) servatae; funiculi nulli; stipes ad 4 mm. longitudine, unde multae rhizomorphae nascuntur; columella arborea, in medio fructificationis percurrens; peridium 520–950 μ crassitudine, cellulis pseudoparenchymatibus ad 16–17 μ diametro metientibus, minoribus extus; gleba purpureo-brunnea, vel nigro-brunnea (teste Thaxtero), "benzo brown to hair-brown" (Ridgway) siccata; septa variabilia, 25–95 μ crassitudine, gelatinosa, hyphis tenuibus, 1 μ diametro contexta hyphis majoribus in septis crassioribus; basidia tetraspora, 25–30 × 5–7 μ, cylindrica, sterigmatibus brevibus; sporae sessilles, 13–16 × 5–6 μ, elongato-ellipsoideae vel ovatae, obtusae.

Type: in Thaxter Herb.

Fructifications up to 2 cm. in diameter, bright, deep lavender, becoming purplish red on handling and dull purplish red when fully matured, drying grayish olive to citrine drab, becoming dull purplish black in alcohol, coloring alcohol and paper purple; fibrils absent; stipe continuous with the columella, up to 4 mm. long, terminating in many branching rhizomorphs; columella dendroid, reaching beyond the center of the fructification; peridium 520–950 μ thick, duplex, outer layer purplish brown, 90–120 μ thick, parenchymatous, composed of smaller cells on the outside, becoming larger within, inner layer 640–830 μ thick, rather falsely pseudoparenchymatous, hyaline or with vinaceous tints, pierced tangentially by large hyphae which are often vesicular and up to 16–17 μ in diameter; gleba purplish brown to blackish brown in fully matured specimens (Thaxter field notes), drying benzo brown to hair-brown after removing from alcohol; septa more hyaline in section than inner peridium, variable in thickness from 25 to 95 μ, gelatinized, composed of small hyaline hyphae 1 μ in diameter; basidia 4-spored, 25–30 × 5–7 μ, cylindrical; spores sessile, 13–16 × 5–6 μ, long-ellipsoidal or tapering toward the basidium, obtuse, vinaceous *in mass.*

This is a beautiful purple species having a duplex peridium of two types of parenchyma, the inner of which has rather large, irregular, intercellular cavities. It approaches *H. Phillipsii* in its radicate base. *H. purpureum* is strikingly distinct from all other species in color and peridial characters.

Specimens examined:

Chile: Magellanes, Punta Arenas, *R. Thaxter, Hypog. 12*, type (in Thaxter Herb. and fragment in Zeller Herb. 7232).

2. **Hysterangium stoloniferum** Tulasne, Ann. Sci. Nat. Bot. II. **19**: 376. 1843; Fung. Hypog. 84–85. 1851; Winter in Rabenhorst, Krypt. Fl. Deutschl. ed. 2, I. **1**: 879. 1883; DeToni in Sacc. Syll. Fung. **7**: 157. 1888; Hesse, Hypog. Deutschl. **1**: 100–101. 1891; Th. M. Fries, Svensk Bot. Tidskr. **3**: 281. 1909; Th. C. E. Fries, Arkiv f. Bot. **17**^{9}: 19. 1921. Pl. 3, fig. 13.

Illustrations: Tulasne, Fung. Hypog. *pl. 11, f. 8;* Fourquignon, Champ. Super. 125; Hesse, Hypog. Deutschl. **1**: *pl. 1, f. 6–9.*

Type: portion in Patouillard Herb. at Farlow Herb.

Fructifications spherical, "the size of a filbert," smooth, white, drying to 4 mm., Isabella color; stipe prolonged into a long cylindrical, solid, white radicle, sparsely branched; columella nearly percurrent, drying 300–400 μ thick; peridium membranaceous, at length subcoriaceous, easily separable, drying 400 μ thick, composed of parenchyma with cells 5–6 μ in diameter; gleba bluish in young material, becoming grayish fuscous and drying cinnamon-buff; cavities elongate, radiating from the whole length of the columella, filled with spores; basidia slender, cylindrical, mostly 2-spored, sterigmata short; spores ellipsoidal, smooth, light yellow under the microscope, dirty brown in mass, 16.6–23.2 × 6–7 μ, mean length 19.7 ± 0.95 μ, appendiculate.

Under decaying oak leaves. Central Europe. Autumn.

The above reference of Hesse is doubtful since he reports the peridium as composed of slender parallel hyphae, larger in diameter toward the outside and tapering towards the gleba.

Specimens examined:

Exsiccati: L. Fuckel, Fung. Rhenani Suppl. 2616.

Hungary: Prencsfalu near Jalsava, *A. Kmet* (in Lloyd Mus. 1921).

Germany: Hessen Nassau, Eisenkaute, *R. Hesse VII, 91* (in Herb. Bot. Inst. Univ. Marburg, as *H. coriaceum*); Rabenkopf bei Oestrich, *L. Fuckel*, Fung. Rhenani Suppl. 2616 (copy in Farlow Herb.).

France: Poitou, near Bonnes, *L. R. Tulasne*, type (portion in Patouillard Herb. at Farlow Herb.).

2a. Var. **rubescens** (Quelet) Zeller and Dodge, n. comb.

Hysterangium clathroides Vittadini var. *rubescens* Quelet, Enchiridion Fung. 246. 1886.—*H. rubescens* Patouillard, Soc. Myc. France Bull. **30**: 351–352. 1914; *not* Tulasne, Ann. Sci. Nat. Bot. **19**: 375. 1843.

H. clathroides Quelet, Soc. d'Emul. Montbéliard, Mem. II. **4**: 375. 1873 [Champ. Jura Vosges **2**: 375. 1873]; *not* Vittadini, Monogr. Tuberac. 13–14. 1831.

H. clathroides Vittadini var. *mutabile* Bucholtz, Soc. Imp. Nat. Moscou Bull. **1907**: 467. 1908; Saccardo & Trotter in Sacc. Syll. Fung. **21**: 495. 1912.

Illustrations: Quelet, Soc. d'Emul. Montbéliard Mem. II. **4**: *pl. 4, f. 5* [Champ. Jura Vosges **2**: *pl. 4, f. 5*].

Type: location unknown to us, type of *H. rubescens* Patouillard in Patouillard Herb. at Farlow Herb.

The variety differs from the species in its becoming grayish red on exposure or to the touch, its gleba being buffy olive instead of cinnamon-buff; spores 21–23 × 6–7 μ.

Under *Quercus* and *Tilia*. France and Russia.

Quelet figures his plant as stoloniferous and small, although he refers it to *H. clathroides*. The material in the Patouillard Herbarium was first determined as *H. clathroides*, then *H. stoloniferum*, before it was published in its present position. (We have been unable to find microscopic characters to separate it from the species.) Variety *mutabile* Bucholtz appears to be the same, although we have not seen the type. It was described with slightly larger spores, 21–23 × 6–7 μ.

Specimens examined:

France: [Jura, between Lons le Saunier and Leponay], *N. Patouillard* (three collections in Patouillard Herb. at Farlow Herb.).

3. Hysterangium neocaledonicum Patouillard, Soc. Myc. France Bull. **31**: 34. 1915; Trotter in Sacc. Syll. Fung. **23**: 598. 1925. Pl. 3, fig. 29.

Type: in Patouillard Herb. at Farlow Herb., Harvard Univ.

Fructifications fleshy, oblong-spherical, 2–3 cm. in diameter, rose-color, becoming brownish in alcohol, each borne on a tough and hard rhizomorph; surface of the fructification costate, marked with furrows rising at the base and extending to the top; peridium membranaceous, easily separable, 120–320 μ thick, pseudoparenchymatous, composed of ovoid cells about 20 μ in diameter; gleba subgelatinous, elastic, ochraceous; columella dendroid, branched; septa radiating from the base, 75–120 μ broad; cavities minute, irregular, filled with spores at maturity; basidia short, 4-, rarely 2-, spored; spores subsessile, ellipsoid-elongate, smooth, almost mucronate at the apex or obtusely rounded, subhyaline, appendiculate, 14–16 × 4–5 μ.

Specimens examined:

Loyalty Islands: New Caledonia, *M. Le Rat*, type (in Patouillard Herb. at Farlow Herb.).

4. Hysterangium coriaceum Hesse, Hypog. Deutschl. **1**: 101. 1891; Saccardo, Syll. Fung. **11**: 168. 1895.

Illustrations: Hesse, Hypog. Deutschl. **1**: *pl. 7, f. 24; pl. 9, f. 5.*

Type: in Herb. Bot. Inst. Univ. Marburg.

Fructifications globose, 1–1.5 cm. in diameter, smooth and white, becoming flesh-red on handling or in light, Verona brown to snuff-brown in alcohol; columella highly developed in the central part of the gleba, light brown; peridium 300–500 μ thick, leathery, easily separable from the gleba, with a very thin outer layer of light brown, closely grouped hyphae; next within, a layer of pseudoparenchyma, thick and violet-colored under the microscope, with another layer of thin-celled, almost colorless hyphae next to the gleba; gleba gray to olive-green, light brownish olive in alcohol, cavities frequently circular in section; septa 130–150 μ thick, composed of hyaline gelatinized hyphae; basidia narrow-cylindrical, mostly 2-spored; sterigmata short; spores 8–12 × 3–4 μ, slightly appendiculate, slightly brownish in mass with a thick epispore.

Under *Betula, Corylus,* and *Fagus silvatica.* Germany. Autumn.

Fructifications turn cherry-red when first placed in alcohol, but the alcohol becomes completely decolorized in a few weeks, and the specimens brownish. Perhaps this species should be regarded as a variety of *H. clathroides,* from which it differs in having a slightly thicker peridium, more brownish gleba, and smaller spores.

Specimens examined:

Germany: Eisenkaute, *R. Hesse* (in Herb. Bot. Inst. Univ. Marburg).

5. **Hysterangium siculum** Mattirolo, Malpighia **14:** 86. 1900; Saccardo & P. Sydow in Sacc. Syll. Fung. **16:** 246–247. 1902; E. Fischer, Ber. d. deut. bot. Ges. **25:** 375. 1907.

Illustrations: Mattirolo, Malpighia **14:** *pl. 1, f. 8–10.*

Type: location unknown to us.

Fructifications globose or depressed-globose, gregarious, white at first, becoming reddish and finally brownish on exposure, coloring alcohol brown; peridium thick, firm, duplex, the outer layer 90–120 μ thick, pseudoparenchymatous, inner layer fibrous, of the same texture as the gleba; gleba bright olivaceous to glauco-virescent; cavities narrow, unequal, mostly linear-elongate, basidia 2–4-spored; sterigmata short; spores ellipsoid, hyaline, smooth, virescent in mass, 18 × 6 μ.

Sicily. April.

Nearest to *H. clathroides,* from which it differs in the texture of the peridium and the size of the spores. Calcium oxalate crystals are often found in the peridium and gleba. *H. siculum* differs from *H. Fischeri* in the duplex peridium and size of spores.

6. **Hysterangium Thaxteri** Zeller & Dodge, sp. nov.

Pl. 2, fig. 5; pl. 3, fig. 28.

Fructificationes ad 1.5 cm. servatae, "russet" vel "Mars brown" (Ridgway); funiculi tenues, copiosi, liberi, concolores; peridium crassum, 2000–3300 μ crassitudine, duplex, strato extero 140–200 μ, hyphis dense compactum, 4–5 μ diametro, strato intero 1860–3160 μ crassitudine, hyphis laxe implexis, 2–4 μ diametro; gleba "argus-brown" (Ridgway); columella recta, 1 mm. crassitudine, cylindrica, non ramosa, in medio gelatinosa; septa 40–45 μ crassitudine, hyphis nodosis, 2–3 μ diametro, laxe implexis; basidia oblongo-clavata, 4–6-spora, 1.5–2 × 7–9 μ, sterig-

matibus brevibus, tenuibus; sporae brunneae acervatae, singulae, hyalinae, ellipsoideae, 3–4 × 1.5–2 μ.

Type: in Thaxter Herb.

Fructifications shrinking to 1.5 cm. in alcohol and glycerine, russet to Mars brown; fibrils slender, abundant, free, concolorous; peridium 2–3.3 mm. thick, duplex, the outer layer 140–200 μ thick, of thick-walled, hyaline, densely woven hyphae 4–5 μ in diameter, inner layer 1860–3160 μ thick, composed of loosely woven, thin-walled hyphae 2–4 μ in diameter, with clamp connections, imbedded in a gel; gleba argus brown; columella straight, 1 mm. thick, cylindric, unbranched, gelatinous in the central third of its diameter; septa 40–45 μ thick, composed of loosely woven, nodose, thin-walled hyphae 2–3 μ in diameter, imbedded in a gel; basidia oblong-clavate, 4–6-spored, 1.5–2 × 7–9 μ; sterigmata short, very fine, about 1 μ long; spores smooth, nearly hyaline singly, but brown in mass, 3–4 × 1.5–2 μ, ellipsoidal.

Brazil and Argentina.

Hysterangium Thaxteri is characterized by its very thick peridium and the nodose hyphae of inner peridium and septa.[1]

Specimens examined:

Argentina: Buenos Aires, *R. Thaxter*, type (in Thaxter Herb.).

Brazil: Rio Grande do Sul, Parecy Novo on Rio Cahy, *J. Rick*, *145* (in Farlow Herb.).

7. **Hysterangium pumilum** Rodway, sp. nov.

Pl. 1, fig. 3; pl. 3, fig. 25.

Hysterangium pumilum Rodway, Roy. Soc. Tasmania Papers & Proc. **1917**: 109. 1918; **1923**: 155. 1924 (English description only).

Fructificationes sphericae, 0.2–0.25 cm. diametro metientes, laeves albidae siccatae; funiculi nulli; columella non prominens; peridium tenue, 30–50 μ crassitudine, simplex, tenuibus brunneis hyphis 2–3 μ diametro contextum; gleba "old gold" vel "Saccardo's olive" (Ridgway); locelli angulares, sporis impletis; septa tenua, 25–60 μ crassitudine, hyphis laxe implexis, 6–7 μ diametro metientibus, non gelatinosa; basidia subclavata, curvata, 35–40 × 10–13 μ, sterigmatibus tenuibus; sporae hyalinae, 14–15 × 4–5 μ, fusiformes, finibus perobtusis.

[1] *Rick, 145*, from Brazil, has been attacked by *Penicillium* sp. and the fructifications disorganized beyond recognition but the texture and color of the peridium and the small spores indicate this species.

Type: in Rodway Herb., cotype in Dodge Herb. and Zeller Herb.

Fructifications spherical, 0.2–0.25 cm. in diameter, smooth, white when dry; fibrils none; columella not prominent; peridium 30–50 μ thick, simplex, composed of slender, thick-walled, brown hyphae 2–3 μ in diameter; gleba old gold to Saccardo's olive; cavities polyhedral, filled with spores; septa 25–60 μ thick, composed of loosely woven, thin-walled hyphae 6–7 μ in diameter, much collapsed and disintegrating in cotype material but not gelatinizing; basidia 35–40 × 10–13 μ, subclavate to curved from procumbent position; sterigmata short; spores hyaline, 14–15 × 4–5 μ, fusiform with very obtuse ends.

In heathy soil. Tasman's Peninsula.

In some of the material the spores have begun to germinate, and in some instances seem to be conjugating in pairs.

Specimens examined:

Tasmania: Wedge Bay, *L. Rodway, 1268*, cotype, *1121* (in Rodway Herb., Dodge Herb. 357, Zeller Herb. 7229, and Lloyd Mus. 082).

8. **Hysterangium Thwaitesii** Berkeley & Broome, Ann. & Mag. Nat. Hist. II. **2**: 267. 1848; Tulasne, Fung. Hypog. 82–83. 1851; Berkeley, Outl. Brit. Fungol. 294. 1860; Cooke, Handb. Brit. Fung. **1**: 358. 1870; DeToni in Sacc. Syll. Fung. **7**: 156. 1888; Hesse, Hypog. Deutschl. **1**: 105. 1891. Pl. 3, fig. 18.

Illustrations: Hesse, Hypog. Deutschl. **1**: *pl. 7, f. 20, 46;* Massee, Ann. Bot. **4**: *pl. 4, f. 80* [Monogr. Brit. Gast. *pl. 4, f. 80*].

Type: in Berkeley Herb. at Kew.

Fructifications 2 cm. in diameter when dry, spherical to somewhat irregular, white, rufous when bruised, drying wood-brown; mycelium white, fibrillose; columella thin, dendroid; fibrils small, nearly free, lighter-colored on the under side of the fructification; peridium 160–180 μ thick, composed of branched, hyaline, gelatinized hyphae 3.5 μ in diameter, underlaid with a sterile portion of the gleba which is composed of thin-walled, parallel hyphae forming a gel as in the septa; gleba Saccardo's olive; cavities long and narrow, filled with spores; septa of thin-walled, parallel

hyphae forming a gel, 90–100 μ thick, basidia not seen; spores rhomboidal, yellowish brown, 17–21 × 6–8 μ.

England.

Specimens examined:

England: near Bristol, *C. E. Broome*, Nov. 1848 (Curtis Herb. at Farlow Herb.); [Leigh Wood, *C. E. Broome*, Aug.] type (in Patouillard Herb. ex Herb. Tulasne at Farlow Herb.).

9. **Hysterangium Rickeni** Soehner, Pilz- und Kräuterfreund **4**: 190–192. 1921; Kryptog. Forsch. **1**: 393. 1924.

Type: in Soehner Herb. but not seen. Authentic material from Soehner in Dodge Herb. and Zeller Herb.

Fructifications spherical, up to 1 cm. in diameter, white to slightly yellowish with a dull reddish tone, finally dirty gray with a violet-brown undertone, drying 0.6 cm., furrowed to scrobiculate, avellaneous; peridium thin, 175–220 μ thick, coriaceous, not easily separable, composed of slender, compact, periclinal hyphae; columella well developed, bluish; gleba at first white with a greenish tone, olive-green when mature, becoming dark green, drying citrine drab; cavities variable in shape; basidia clavate to cylindrical, 2-spored, slender, 28–35 × 4–7 μ; paraphyses smaller but up to 10 μ broad; spores hyaline, yellow to olive-green in mass, 15–18 × 6–7 μ, occasionally less than 15 μ or up to 20 μ, 1–3-guttulate.

Under *Fagus*. Central Europe. June to August.

The above description is based on Soehner's forma *fagorum* which was first and more fully described.

Forma **pinetorum** Soehner, Pilz- und Kräuterfreund **4**: 191. 1921.

This form in pine woods is distinguished by a brighter gray-green, more fragile gleba, more yellowish columella, and non-guttulate spores.

Under *Pinus*. Bavaria. September to November.

The specimen from Salzburg, cited below, was collected in pine woods.

Specimens examined:

Austria: Salzburg, *E. Soehner, 1045* (in Soehner Herb. and Dodge Herb.).

Germany: Bavaria, Pöpplinger Heide bei München, *E. Soehner, 1014* (in Soehner Herb. and Dodge Herb.).

10. Hysterangium fragile Vittadini, Monogr. Tuberac. 14. 1831; Tulasne, Fung. Hypog. 84. 1851; Winter in Rabenhorst, Krypt.-Fl. Deutschl. ed. 2, I. **1**: 879. 1883; DeToni in Saccardo, Syll. Fung. **7**: 156–157. 1888; Hollós, Magyarorszag Földalatti Gombai, 88–89. 1911; ? Hesse, Hypog. Deutschl. **1**: 103–104. 1891; Soehner, Krypt. Forsch. **1**: 392. 1924.

Illustrations: Vittadini, Monogr. Tuberac. *pl. 4, f. 15;* ? Hesse, Hypog. Deutschl. **1**: *pl. 7, f. 22.*

Type: location unknown to us.

"Fructifications subglobose, without fibrils ? ; peridium thick, very fragile, yellow without, bare, granulose, farinose; gleba very soft, ashy, becoming greenish; cavities irregular, scarcely visible; odor, when fresh, that of *Tuber Borchii;* about the size of a filbert; peridium soft, thick, white within, reminiscent of the cortex of the stipe of *Verpa digitaliformis,* easily separating from the gleba. A gelatinous layer attaching the peridium to the gleba is very thick, hence the mature gleba is very soft and subdeliquescent. When mature and freshly dug, the peridium cracks off as easily as the shell of a sparrow's egg.

"In oak woods near the Po River, under fallen leaves, half buried; winter. It has been found by me twice. This species has the surface color of *H. clathroides,* the softness of the flesh of *H. membranaceum;* it differs from both in the nature of the peridium, odor, habitat and season."—Vittadini.

Hesse, who reports finding this species twice on Dammelsberg near Marburg, gives the following characters: peridium 1.5 mm. thick, composed of richly septate and branched hyphae; cavities small; septa broad; basidia cylindrical, 2–3-spored; spores slightly appendiculate, 12 × 4 μ, gray-green in mass. Soehner reports several collections agreeing with Hesse's description, spores 10–12.5 × 3–4 μ. Hollós reports several collections from Hungary agreeing with Hesse, giving spores 12–16 × 4–5 μ. This material seems to belong to a distinct species but we prefer not to name it until more material is available.

Hollós, after studying a fragment of the type, states that the

spores are 22–24 × 7–8 μ, peridium red-spotted, drying very thin, and regards *H. fragile* Vitt. as a possible synonym of *H. stoloniferum* Tul. Tulasne reports the spores 23 × 6.4 μ, practically obliterating the cavities.

11. Hysterangium calcareum Hesse, Hypog. Deutschl. **1**: 97. 1891; Saccardo, Syll. Fung. **11**: 168. 1895. Pl. 3, fig. 15.

Illustrations: Hesse, Hypog. Deutschl. **1**: *pl. 7, f. 21, 23; pl. 9, f. 15.*

Type: probably in Bot. Inst. Univ. Marburg; not seen, although other material determined by Hesse was studied.

Fructifications globose, the size of a hazel-nut, grayish white; columella branched, penetrating to the middle of the fructification; peridium fleshy when young, becoming fragile and papery, 0.6 mm. thick, composed of an outer layer of grayish white, thin-walled hyphae, a layer of brownish yellow hyphae, a layer of coarse, loosely woven, septate, hyaline hyphae, and another very thin layer of slender brownish yellow, periclinal hyphae; gleba bluish to olive-green; cavities narrow, much longer than broad, at first empty, later filled with spores; septa thinner than in *H. rubricatum*, cartilaginous; basidia cylindric, 2-spored; spores broad-ellipsoidal, 11–13 × 4–5 μ, hyaline, gray-green in mass, appendiculate, epispore thin at first, thickening with age.

In calcareous soil in birch woods. Germany and Czechoslovakia. Summer.

This species differs from *H. clathroides* in structure of the peridium, form and size of the spores, and the longer cavities, and from *H. rubricatum* in lack of a reddish color in the peridium.

Specimens examined:

Czechoslovakia: Mähren, Zwittau, *J. Hruby* (in Hesse Herb. at Bot. Inst. Univ. Marburg).

12. Hysterangium Petri Mattirolo, Malpighia **14**: 262–263. 1900; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 247. 1902.

Type: location unknown to us.

Fructifications globose, white, lightly spotted with yellow, unchanging, varying in size from that of a pea to that of a filbert; columella central, gelatinous, little developed; peridium easily

separable, fibrous, composed of thick-walled hyphae; gleba grayish virescent; cavities minute-elongate; basidia 2-spored, cylindrical; spores ovate-elongate, smooth, hyaline, 11–14 × 4–5 μ; odor weak.

In chestnut groves. Italy. April.

This species is nearest *H. Thwaitesii*, from which it differs by the yellow color of the peridium, which remains unaltered in alcohol or on drying, and in the size of the spore.

DOUBTFUL SPECIES

1. **Hysterangium viscidum** Massee & Rodway, Kew Bull. Misc. Inf. **1898:** 127. 1898; Saccardo & P. Sydow in Sacc. Syll. Fung. **16:** 246. 1902; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911:** 27–28. 1912; **1923:** 155. 1924.

Illustrations: Rodway, Roy. Soc. Tasmania Papers & Proc. **1911:** *pl. 3, f. 8.*

Type: not seen.

"Fructifications irregular, oblong, chestnut-color, viscid, 3 × 1.5 cm.; peridium thick, tough, easily separable from the gleba; gleba pale at first, dark brown in age; cavities radiating from the base, small, irregular; septa thick, brown, not scissile; basidia 3–4-spored; spores broadly oblong-ellipsoidal, obtuse at both ends, 12–15 × 8–10 μ, minutely papillate, yellowish brown to dirty brown in mass.

"In gullies near Hobart, *L. Rodway, 270.*

"Readily distinguished in the genus by the chocolate brown, viscid peridium and elliptic oblong, obtuse spores."—Massee & Rodway.

It seems quite probable that this species belongs in the genus *Hymenogaster*, and in the group of species of that genus with viscid peridia, for nearly all the characters given in the meagre description are very unusual in the genus *Hysterangium*. However, since we have not seen the type nor any material surely referable there, we prefer to leave this among the doubtful species.

Cleland's collection, No. 16, National Park, S. Australia, agrees with the above description in all respects. It is also referable to *Hymenogaster nanus* Massee & Rodway, 1899.

2. **Hysterangium fusisporum** Massee & Rodway, Kew Bull. Misc. Inf. **1898**: 127. 1898; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 247. 1902; Rodway, Roy. Soc. Tasmania Papers & Proc. **1911**: 26. 1912; **1923**: 155. 1924.

Type: probably at Kew Herb. but not seen.

Subglobose, irregular, 1.5–2 cm. in diameter, smooth, very thin, white to yellow-spotted, hyaline within; peridium not separable; gleba firm, pale; cavities small, irregular, sinuous; spores fusiform, smooth, 20–22 × 8 μ, hyaline; basidia 2-spored; sterigmata short.

Habitat, subterranean, Tasmania (*Rodway*).

While we have not seen the type, material sent us by Rodway should be referred to *Hymenogaster*. Further consideration of these species may be deferred until we have seen the type.

EXCLUDED SPECIES

1. **Rhizopogon Marchii** (Bresadola) Zeller and Dodge, comb. nov.

Hysterangium Marchii Bresadola, Fung. Trident. **2**: 99. 1900; Saccardo & P. Sydow in Sacc. Syll. Fung. **16**: 246. 1902; Bataille, Soc. Myc. France Bull. **39**: 166. 1923.

Illustrations: Bresadola, Fung. Trident. **2**: *pl. 211, f. ii.*

Type: portion of type in Dodge Herb.

Fructifications irregularly depressed-globose, 2–3.5 × 1–2 cm., color Natal brown when moist, drying avellaneous to wood-brown (Isabella color in Bresadola's plate); rooting fibrils few, large; columella branching almost at the base of the fructifications, slender, inconspicuous; peridium 180–230 μ thick, stupose, composed of granulose, large, thin-walled, yellow-brown hyphae 5–8 μ in diameter, loosely woven toward the outside, slightly smaller and more compactly woven within; gleba buffy citrine, cavities very small, irregular, filled with spores; septa 140–160 μ, composed of slender, thin-walled hyphae 3–5 μ in diameter, becoming highly gelatinized at maturity; spores acrogenous, old gold, ellipsoidal, often truncate at the base, 8–11 × 4–5.5 μ, smooth. No odor.

Under *Pinus nigra* near Trieste. September.

Specimens examined:

Italy: Trieste, Verla, *I. Marchi*, type (in Bresadola Herb. and in Dodge Herb.).

2. Rhizopogon niger (Lloyd) Zeller & Dodge, comb. nov.

Hysterangium niger Lloyd, Myc. Notes 68: 1173. 1923, nom. nud.; Verwoerd, S. African Jour. Sci. **22**: 163. 1925.

Illustrations: Lloyd, Myc. Notes 68: *f. 2325*.

Fructificationes depresso-sphaeroideae, subirregulares, 3 × 1 × 1.5 cm. diametro metientes, nigrae; peridium tenue, 75–100 μ crassitudine, stuppeum, hyphis nigro-brunneis, 2–3 μ diametro, subparallelibus contextum; gleba "Brussels brown" (Ridgway); locelli parvi, angulares, vacui; septa circa 40–50 μ crassitudine, gelatinosa, cellulis ellipsoideis vel sphericis, facile tinguentibus impletis, strato medio cellulis elongatis facile tinguentibus; basidia filiformia, trispora; sporae brunneae acervatae, ellipsoideae, 7–9 × 2–3 μ.

Type: in Lloyd Museum, in Dodge Herb., and in Zeller Herb.

Fructifications depressed-spheroidal to somewhat irregular, perhaps due to the coalescence of several fructifications, drying 3 × 1 × 1.5 cm., black without, covered with adhering sand grains; peridium 75–100 μ thick, stupose, composed of dark brown, thick-walled, nearly parallel hyphae 2–3 μ in diameter; gleba Brussels brown; cavities small, angular, empty; septa about 40–50 μ thick, highly gelatinized, traversed through the middle by a layer of deeply staining, closely woven hyphae, the remainder of the gelatin filled with irregularly placed, ellipsoidal to spherical, deeply-staining cells, which seem to have no visible connection either with the central strand or with each other; basidia narrow, filiform, crowding out between the superficial, gelatinized cells of the septa, mostly 3-spored; spores brown in mass, slender, ellipsoidal, 7–9 × 2–3 μ.

South Africa.

Superficially this species looks like *Rhizopogon piceus;* the color and texture of the gleba is much as in *R. pachyphloeus*, but micsoscopically it is easily distinguishable from either.

Specimens examined:

South Africa: Knysna, *Miss A. V. Duthie*, type (in Lloyd Mus. 081, in Dodge Herb. 353, and in Zeller Herb. 7246).

3. Hysterangium ? Pseudo-Acaciae (Fries) DeToni in Sacc. Syll. Fung. **7**: 159. 1888.

Mylitta Pseudacaciae Fries, Syst. Orb. Veg. **1**: 154. 1825; Syst. Myc. **3**: 226. 1829.

Mylittaea Pseudo-Acaciae Cesati in Rabenh. Klotzschii Herb. Viv. Myc. **16**: No. 1549. 1851 (with description).

This species was evidently based on the nodules of *Robinia Pseudacacia,* caused by *Rhizobium* sp., according to the collection of Cesati cited below, confirming the opinion of Mattirolo, Che cosa é la Mylitta Pseudo-Acaciae Fries ? Soc. Bot. Ital. Bull. **1924**: 13–16. 1924. If a study of Chaillet's specimen in Fries' herbarium (the type) should confirm this, *Mylitta* and its variant *Mylittaea* should be dropped as based on a mixture of parasite and host in accordance with article 51, section 4a, of the International Rules of Nomenclature. It is probable that DeToni referred this species to *Hysterangium* without having seen a specimen, since certain phrases of the original descriptions suggest this genus.

Specimens examined:

Italy: Piemonte, Vercelli, *V. Cesati* in Rabenhorst, Klotzschii Herb. Viv. Myc. **16**: 1549 (in Farlow Herb.).

ERRATA

Since correcting proof of this article, we have found that A. Trotter, in the supplement to the last section of volume 24 of Saccardo's 'Sylloge,' has translated descriptions by Rodway.

Page 84, last paragraph, line 2, insert 8 instead of 11.

Page 97, line 23, page 98, line 22, and page 115, line 25, delete "sp. nov." and add "apud Trotter in Sacc. Syll. Fung. **24**: 1327. 1928."

Explanation of Plate

PLATE 1

Fig. 1. *Hysterangium album* Zeller & Dodge.
Section of peridium and gleba showing their structure and relation to each other. From type material. × 42.5.

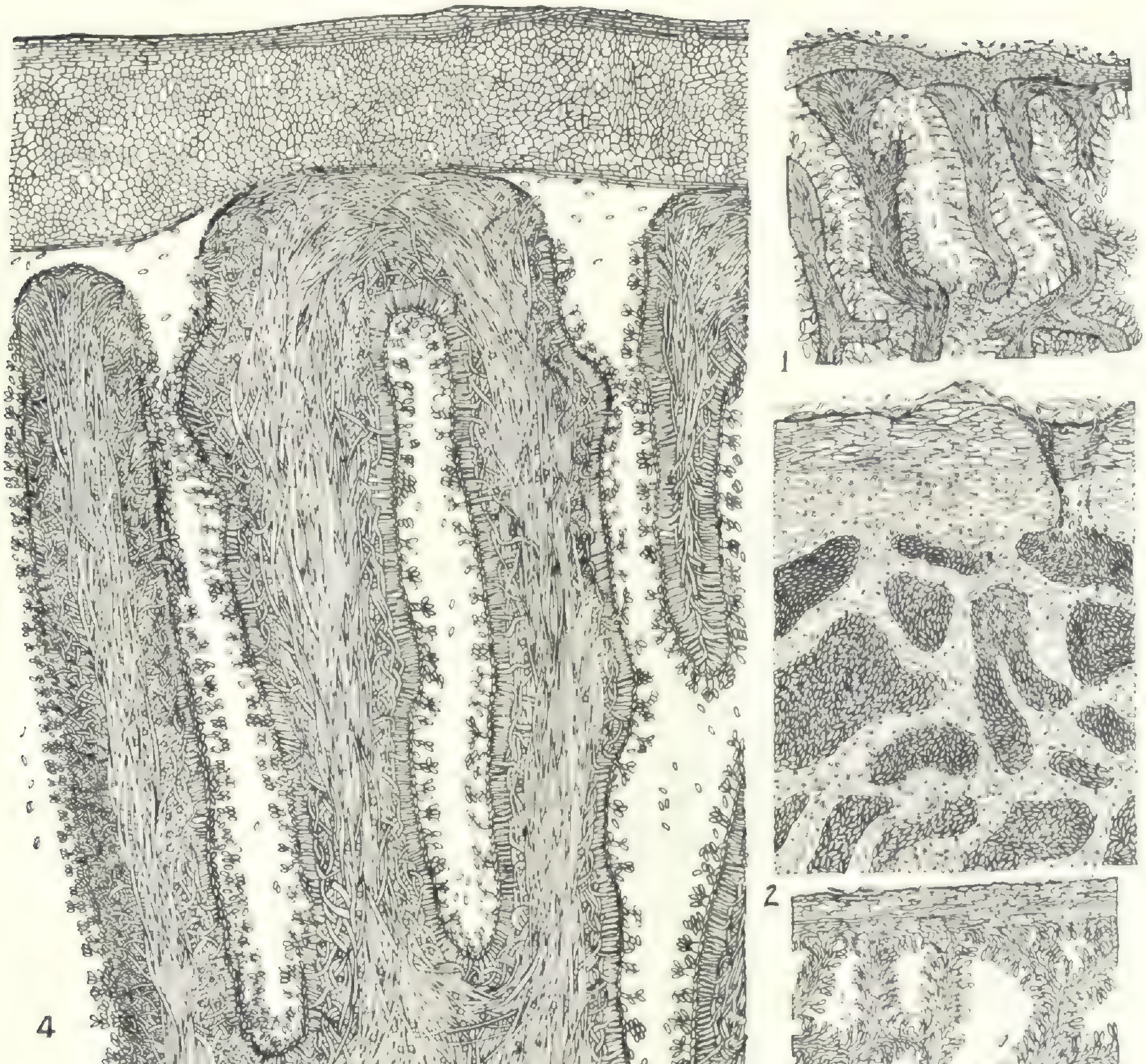
Fig. 2. *Hysterangium Fischeri* Zeller & Dodge.
Section showing structure of peridium and gleba and their relation. The peculiar pores extending from glebal cavities to the surface of the fructifications were not infrequently found in the type material, but may not be a constant character. × 42.5.

Fig. 3. *Hysterangium pumilum* Rodway.
Section showing the relation of the peridium to the gleba, the simple structure of the septa, and the pseudoparenchyma of the peridium. Drawing made from cotype material. × 42.5.

Fig. 4. *Hysterangium crassirhachis* Zeller & Dodge.
Section showing the parenchyma of the easily-separable peridium and the structure of the very broad, radiating septa. Drawing made from type material. × 42.5.

Fig. 5. *Hysterangium purpureum* Zeller & Dodge.
Section of the peridium and gleba showing their close relation to each other, the two types of parenchyma of the peridium, both of which are penetrated periclinally by lacunae. The septa are gelatinous. Drawing from type material. × 42.5.

Fig. 6. *Hysterangium strobilus* Zeller & Dodge.
Section showing the outer, fibrous layer which is more readily separable from the inner, parenchymatous layer of the peridium than is the latter from the gleba. Drawing from type material. × 42.5.



ZELLER AND DODGE—HYSTERANGIUM IN NORTH AMERICA

Explanation of Plate

PLATE 2

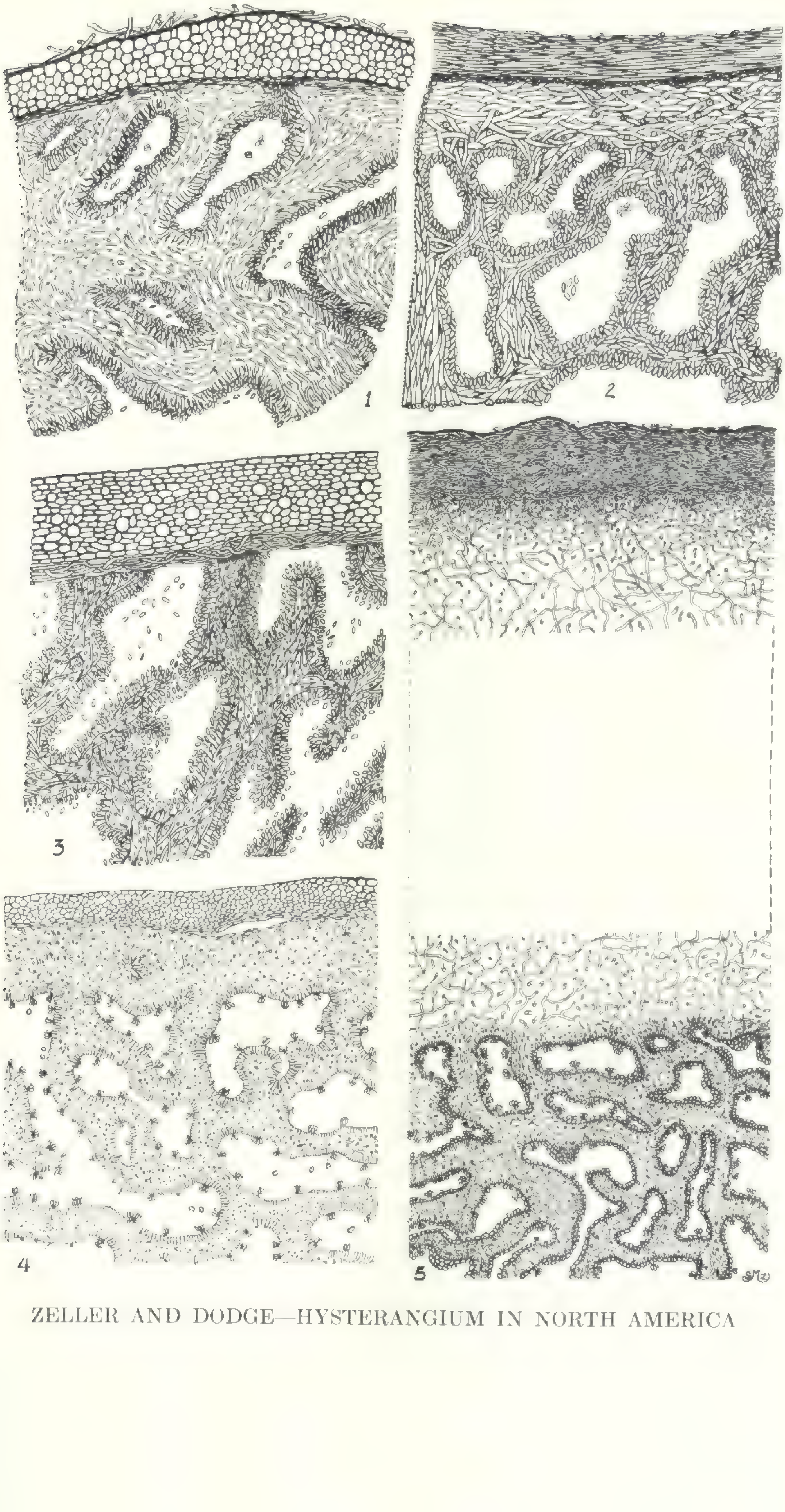
Fig. 1. *Hysterangium affine* Massee & Rodway.
Section showing parenchyma of the peridium and the relation of the latter to the gleba. Drawing from Rodway's Tasmanian collection No. 1261. × 42.5.

Fig. 2. *Hysterangium cistophilum* (Tulasne) Zeller & Dodge.
Section showing the fibrous structure of the peridium and the layer of glebal tissue beneath it. Drawing from Zeller's Oregon collection No. 7197. × 42.5.

Fig. 3. *Hysterangium clathroides* Vittadini.
Section of peridium and gleba showing the separable character of the peridium along the inner side of a thin fibrous layer beneath the major parenchymatous portion. Drawing from Zeller's Oregon collection No. 2582. × 42.5.

Fig. 4. *Hysterangium inflatum* Rodway.
Section showing the rather thin parenchymatous peridium, the very thin film of pseudoparenchyma between it and the gleba, and the thick, underlying, sterile, glebal layer. The peridium separates from the gleba along the line of pseudoparenchyma. Drawing from Rodway's Tasmanian collection No. 1267, which is labeled "cotype." × 42.5.

Fig. 5. *Hysterangium Thaxteri* Zeller & Dodge.
Section of the peridium and gleba showing the very thick gelatinous layer of peridium and the thinner fibrous outer layer (rind). The hyphae of the gelatinous layer are suspended in a hyaline gel. Note the peculiar clamp-connections of the inner peridial layer and tramal tissues of the septa. Drawing from Dr. Thaxter's Argentine type collection. × 42.5.



ZELLER AND DODGE—HYSTERANGIUM IN NORTH AMERICA

Explanation of Plate

PLATE 3

Fig. 1. *Hysterangium occidentale* Harkness.

Section of the peridium and gleba showing their relation and structure. The outer peridial layer of loosely interwoven hyphae overlies a layer which is a peculiar mixture of parenchyma and pseudoparenchyma. A thin fibrous layer separates peridium and gleba. The septa and main percurrent branches of the columella are thick and of a gelatinous structure. Drawing from Oregon material (Zeller, 7063). × 42.5.

Fig. 2. *Hysterangium neglectum* Massee & Rodway.

Section showing structure of the peridium and gleba, and section of one percurrent branch of the columella. The peridium is composed of two distinct layers of pseudoparenchyma. Drawing from Tasmanian material (Rodway, 614, cotype). × 42.5.

Fig. 3. *Hysterangium obtusum* Rodway.

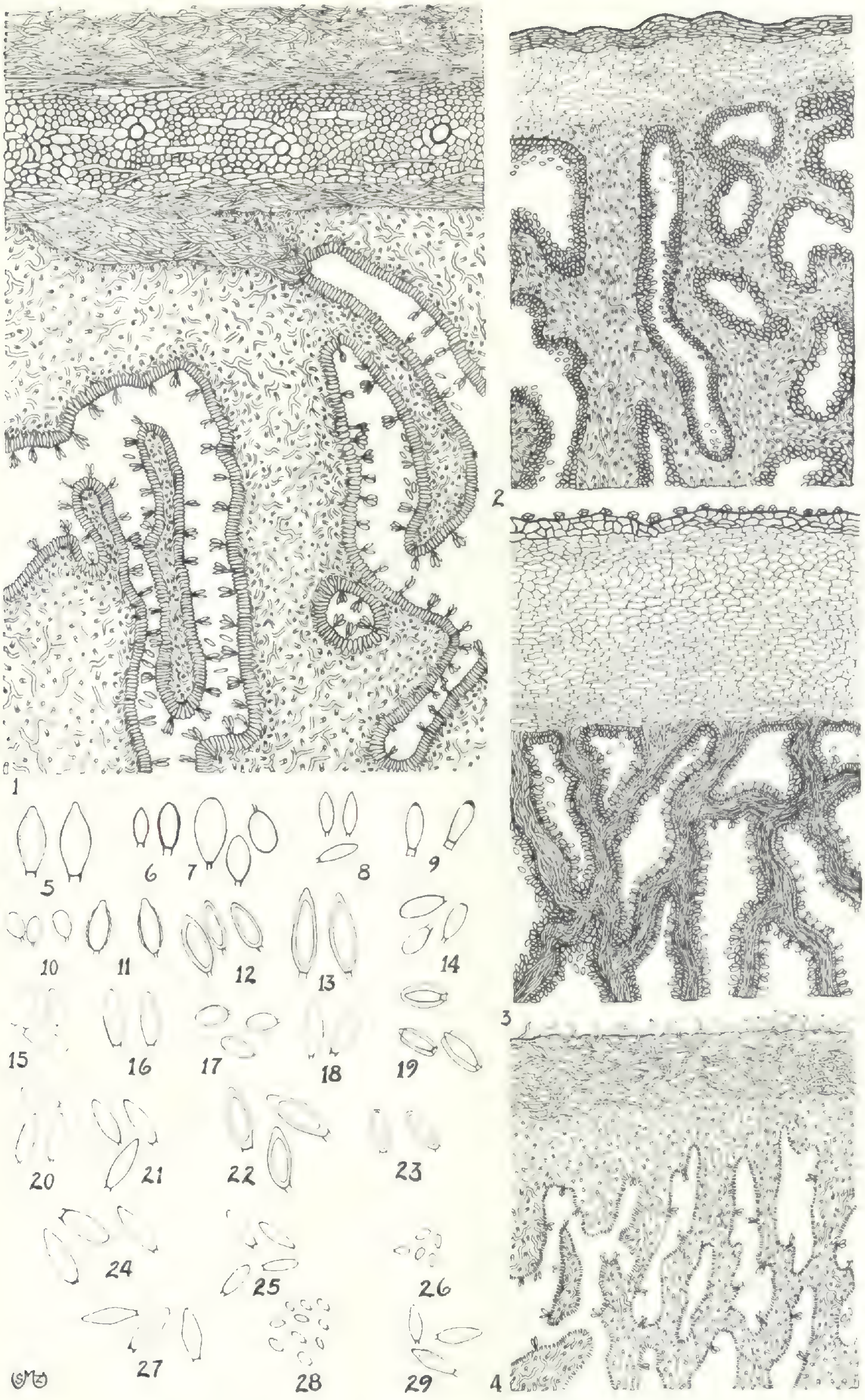
Section of the thick peridium of spongy pseudoparenchyma which is mixed with some parenchyma but as a whole not in definite layers. The outer rind is almost distinct because of color and heavy cell walls. The septa of the gleba are fibrous in structure. Drawing from Tasmanian material (Rodway, 1264, cotype). × 42.5.

Fig. 4. *Hysterangium fuscum* Harkness.

Section showing the fibrous structure of the peridium and its relation to the underlying layer of sterile glebal tissue. Drawing from Parks' Californian collection, No. 1167. × 42.5.

Figs. 5–29. Outline drawings to show relative size and form of various species of *Hysterangium*. All, × 500.

- Fig. 5. Spores of *H. album* Zeller & Dodge.
- Fig. 6. Spores of *H. affine* Massee & Rodway.
- Fig. 7. Spores of *H. neglectum* Massee & Rodway.
- Fig. 8. Spores of *H. Fischeri* Zeller & Dodge.
- Fig. 9. Spores of *H. occidentale* Harkness.
- Fig. 10. Spores of *H. obtusum* Rodway.
- Fig. 11. Spores of *H. strobilus* Zeller & Dodge.
- Fig. 12. Spores of *H. clathroides* Vittadini.
- Fig. 13. Spores of *H. stoloniferum* Tulasne.
- Fig. 14. Spores of *H. fuscum* Harkness.
- Fig. 15. Spores of *H. calcareum* Hesse.
- Fig. 16. Spores of *H. nephriticum* Berkeley.
- Fig. 17. Spores of *H. membranaceum* Vittadini.
- Fig. 18. Spores of *H. Thwaitesii* Berkeley & Broome.
- Fig. 19. Spores of *H. inflatum* Rodway.
- Fig. 20. Spores of *H. crassirhachis* Zeller & Dodge.
- Fig. 21. Spores of *H. purpureum* Zeller & Dodge.
- Fig. 22. Spores of *H. cistophilum* (Tulasne) Zeller & Dodge.
- Fig. 23. Spores of *H. Pompholyx* Tulasne.
- Fig. 24. Spores of *H. Harknessii* Zeller & Dodge.
- Fig. 25. Spores of *H. pumilum* Rodway.
- Fig. 26. Spores of *H. Phillipsii* Harkness.
- Fig. 27. Spores of *H. rubricatum* Hesse.
- Fig. 28. Spores of *H. Thaxteri* Zeller & Dodge.
- Fig. 29. Spores of *H. neocaledonicum* Patouillard.



ZELLER—HYSTERANGIUM IN NORTH AMERICA

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VARIATION IN ASTER ANOMALUS

EDGAR ANDERSON

Geneticist to the Missouri Botanical Garden
Assistant Professor of Botany in the Henry Shaw School of Botany of Washington University

Table of Contents

I. Introduction
II. Taxonomy and morphology
III. Variation
IV. Experimental data
V. Summary and conclusions
VI. Bibliography

I. Introduction

Among the higher plants relatively few species have been so intensively studied and described that the interested reader can gain a clear morphological conception of the species as a whole. The dearth of such information would seem to be one of the main reasons why modern biologists have such widely divergent views as to the nature of species. Most of our data on the species problem have been gleaned indirectly from taxonomic work. But taxonomists have been interested mainly not in the nature of species but in the practical classification of the groups with which they were working. Considering the enormous number of groups still awaiting monographic treatment they have probably been wise in applying themselves to the task in hand and eschewing theoretical considerations.

It has, however, seemed to the writer that the nature of species may very properly be taken up as a study in itself, to be investigated for its own sake. It may be that a closer analysis will only reveal the hopeless complexity of the problem and the impossibility of establishing any generalizations. On the other hand, it seems possible that morphological relationships between the individuals which go to make up a species may be uniform enough to yield important generalizations upon further study.

With this end in view, a few relatively simple Linnaean species have been intensively studied as to their morphology, geographical distribution, and the genetic relationships within the species and with other species. The main body of the work has been confined to the genus *Iris*, and it was therefore thought wise to study a few other species from widely separated groups of plants. *Aster anomalus* Engelm. was one of those chosen, for though it belonged to one of the most difficult genera in the Compositae it seemed to be a simple, well-differentiated species. The following data are admittedly meagre in several respects, but no further work is being planned with the species because of inherent technical difficulties in making controlled pollinations, raising large numbers of seedlings, etc. The following brief account does at least present a small body of codified information for one species of the genus *Aster*, a group where such information, though badly needed, is practically non-existent.

ACKNOWLEDGMENTS

For much helpful information on taxonomic points the author is deeply indebted to his colleague, Dr. J. M. Greenman. For the loan of herbarium specimens from the Field Museum and the Gray Herbarium he is greatly obliged to the curators of those institutions. Dr. J. Paul Goode has kindly allowed the use of his copyrighted map in fig. 1.

II. Taxonomy and Morphology

Aster anomalus Engelm. in Torr. & Gray, Fl. N. Am. **2**: 503. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 181. 1884; Gray's Manual, ed. 7, 807. *fig. 936.* 1908; Britton & Brown, Ill. Flora, ed. 2, **3**: 413. *fig. 4296.* 1913; Small, Fl. Southeast. U. S., ed. 2, 1213. 1913.

Slender herbaceous perennials, somewhat pubescent and scabrous, 2-10 dm. high; stems simple or racemosely branched above; young leaves ovate, often deeply serrate, purplish beneath; cauline leaves firm in texture, entire or occasionally subserrate, the lower leaves ovate to ovate-lanceolate, deeply cordate at the base, on slender naked petioles, the upper ones small, subsessile; heads large, hemispherical; involucre several-seriate, bracts acute, appressed at the base, apex strongly reflexed; rays 20–45, bright lavender-blue; achenes brownish, glabrous, ovate-lanceolate, with 3–5 prominent ribs; pappus brownish.

Aster anomalus is marked by its peculiar combination of characters. In common with its closest relatives, *A. azureus* Lindl. and *A. Shortii* Lindl., it has bright blue flowers and cordate lower leaves of firm texture. Unlike them, it has a large number of ray-flowers and strongly reflexed involucral bracts. The resulting combination is unlike any other member of the genus and was well described (Torr. & Gray, Fl. N. Am. **2**: 503. 1843) in a note appended to the original description: "A most remarkable species with nearly the foliage of *Aster Shortii* while the heads and involucre much resemble those of *A. oblongifolius.*"

It is a species of limited distribution, being found on limestone hills and cliffs from central Illinois, across Missouri, to adjacent parts of Kansas, Oklahoma, and Arkansas.

Specimens examined:

(The following abbreviations indicate the herbaria in which the specimens occur: FM = Field Museum; GH = Gray Herbarium; MBG = Missouri Botanical Garden).

Illinois: Carlinville, Sept. 11, 1889, *Andrews* (MBG); same locality, Sept. 4, 1890, *Andrews 1* (GH); Athens, Sept. 1868, *Hall* (FM); Peoria, Sept. 1891, *McDonald* (FM); same locality, Sept. 1890, *McDonald* (MBG); Schuyler Co., Sept. 13, 1872, *Mead 4* (FM); Falling Spring, Sept. 1844, *Engelmann* (MBG); Prairie du Pont, Sept. 1842, *Engelmann* (MBG).

Missouri: Allenton, Oct. 10, 1890, *Letterman* (MBG); Hannibal, Sept. 16, 1911, *Davis 1050* (MBG); Clarksville, Sept. 24, 1911, *Davis 1120* (MBG); Branson, Oct. 20, 1907, *Palmer T4* (MBG); Kimmswick, Sept. 27, 1885, *Wislizenus 172* (MBG); Monteer, Oct. 10, 1907, *Bush 4889* (MBG); Swan, Sept. 24, 1905, *Bush 3417* (MBG); Eagle Rock, Sept. 23, 1896, *Bush 297* (MBG); Belleville, Sept. 22, 1908, *Palmer 1339* (MBG); La Grange, Sept. 6, 1915, *Davis 6248* (MBG); Jasper, Oct. 7, 1908, *Palmer 1334* (MBG); Joplin, Oct. 30, 1908, *Palmer 1416* (MBG); Reddings Mill, Sept. 26, 1906, *Bush 5194* (MBG); Fenton, Oct. 9, 1921, *Drushel 4590* (MBG); Jerome, Sept. 25, 1912, *Kellogg* (MBG); Van Buren, Oct. 11, 1920, *Palmer 19471* (MBG); Williamsville, Oct. 20, 1907, *Bush 1107* (MBG); Ironton, Oct. 13, 1920, *Palmer 19531* (MBG); Carl Jct., Oct. 7, 1908, *Palmer 1338* (MBG); Club House, Sept. 11, 1897, *Trelease 702* (MBG);

Oregon Co., Aug. 14, 1893, *Bush* (MBG); McDonald Co., Sept. 1, 1893, *Bush* (MBG); Pond, Oct. 6, 1918, *Aiken* (MBG); Galena, Oct. 11, 1913, *Palmer 4628* (MBG); Pilot Knob, Nov. 1845, *Engelmann* (MBG); Kimmswick, Oct. 11, 1863, *Engelmann* (MBG); Meramec Highlands, Sept. 1843, *Engelmann* (MBG); Dr. Engelmann's garden, Oct. 15, 1872, *Engelmann* (MBG); Seligman, Oct. 24, 1925, *Palmer 29374* (MBG); Greene Co., Sept. 4, 1893, *Bush 142-A* (FM).

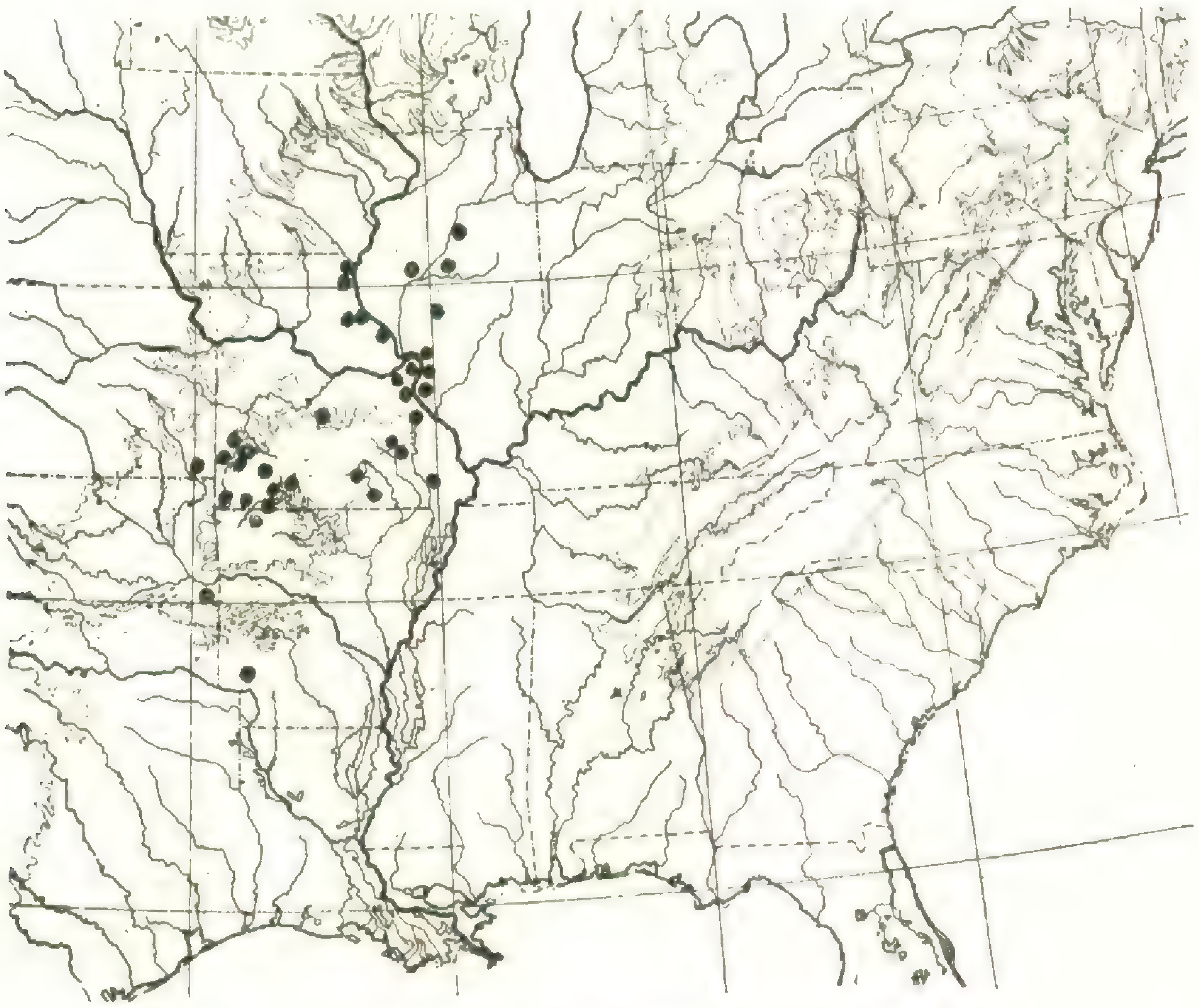


Fig. 1. Geographical distribution of *Aster anomalus*.

Arkansas: McNab, Oct. 19, 1915, *Palmer 8969* (MBG); same locality, Oct. 5, 1923, *Greenman 4440* (MBG); Eureka Springs, Sept. 19, 1913, *Palmer 4367* (MBG).

Kansas: Baxter Springs, Oct. 5, 1925, *Palmer 29029* (MBG).

Oklahoma: Poteau, Oct. 28, 1915, *Palmer 9055* (MBG).

The distribution of the species as shown by the above specimens is illustrated in fig. 1.

III. Variation

In general it may be said that while *Aster anomalus* is extremely variable, the variation centers about what Sinskaya ('28) calls,

"a nucleus of common features." Among all the plants examined, including herbarium specimens, plants studied in the field, and over 200 seedlings grown in the experimental plot, there was not a single individual whose specific identity was questionable. All of them were unmistakably *Aster anomalus*. The variation extended to all parts of the plant; leaf number, size, and shape; flower-head number, size, shape, and arrangement; ray number, size, shape, and color; etc. Three characters were studied in some detail: the lower cauline leaves, the flower-heads, and the ripened achenes.

Fig. 2. Outlines of *Aster anomalus*, *A. azureus*, and *A. Shortii* (reading from left to right).

The cauline leaves.—The lower cauline leaves of *Aster anomalus* are very similar to those of the closely related species, *A. Shortii* and *A. azureus*. The leaves of all three species are firm in texture and are ovate or ovate-lanceolate with a cordate base. While they agree on these major points they differ on many minor ones, and *Aster anomalus* can be successfully separated from its

closest relatives (or from all the other species of the genus for that matter) by leaf characters alone. Figures 2 and 3 show the main differences between the leaves of the three species. In fig. 2 are typical silhouettes reconstructed from tracings of herbarium specimens. It may be seen that *A. azureus* differs

Fig. 3. Variation in outline of lower cauline leaves: upper row, *Aster azureus;* middle row, *A. anomalus;* lower row, *A. Shortii.*

from the other two species in having fewer leaves with only the lowermost cordate at the base and proportionately longer petioles. These differences hold generally for the three species in question.

In fig. 3 are shown tracings of leaf blades from eight specimens

of each species. These figures demonstrate that the leaves of *A. anomalus* are more deeply cordate at the base than those of either of the other species. They are also, on the average, less pronouncedly lanceolate than those of *A. Shortii.* From *A. azureus,* in addition to the differences reported above, they are further differentiated by more deeply cordate bases and an almost entire lack of serrations. All of these differences are summarized in table I.

TABLE I

COMPARISON OF CAULINE LEAVES IN THREE SPECIES OF ASTER

A. azureus	*A. anomalus*	*A. Shortii*
Cordate bases on only the lowermost caulines	Cordate bases on most of the large caulines	Cordate bases on most of the large caulines
Petioles proportionately long	Petioles proportionately short	Petioles intermediate
Leaves ovate to ovate-lanceolate	Leaves ovate to ovate-lanceolate	Leaves ovate-lanceolate
Leaf bases cordate or subcordate	Leaf bases deeply cordate	Leaf bases cordate or subcordate
Leaves often serrate	Leaves entire or at most subserrate	Leaves entire or at most subserrate

Flower-heads.—In *Aster anomalus* all the flower-heads of a single individual are usually very similar. Numbers b, c, f, of fig. 4, pl. 4, show three heads from the same plant. It will be noticed that they agree in having numerous rays, which are relatively short, blunt, and regular in outline. On the other hand, the differences between flower-heads on separate plants are very conspicuous. Among the characters which differentiate individuals are: length of rays, number of rays, shape of rays (cleft or not cleft, broad or narrow, straight or waved, etc.),

TABLE II

NUMBER OF RAYS ON INDIVIDUALS OF TWO WILD POPULATIONS COMPARED WITH THAT OF EXPERIMENTAL POPULATION, SBCZG. SBCZG WAS COMPOSED OF SIXTEEN SISTER PLANTS GROWN FROM SEED COLLECTED FROM A SINGLE INDIVIDUAL AT HIGH RIDGE, MO.

	Number of rays													
	19	20	21	22	23	24	25	26	27	28	29	30	31	32
High Ridge, Mo.			1				1	2			1	1		1
Rankin, Mo.		1	1		1					1			2	1
Sbczg	1	2		2	1	1	2	3	1		1	2		

TABLE III

LENGTH OF RAY (LIGULE) IN MM. FOR THE SAME INDIVIDUALS REPORTED IN TABLE III

	Length of ray										
	6	7	8	9	10	11	12	13	14	15	16
High Ridge, Mo.			1		2	1		2	1		
Rankin, Mo.		1				1	1	1	2		1
Sbczg		1	2	2	3	4		3	1		

width of disk, number of disk-flowers, etc. Exact determinations of ray number and ray length were made for two small populations and are summarized in tables II and III. The correlation

TABLE IV

CORRELATION BETWEEN NUMBER OF RAYS AND LENGTH OF RAY

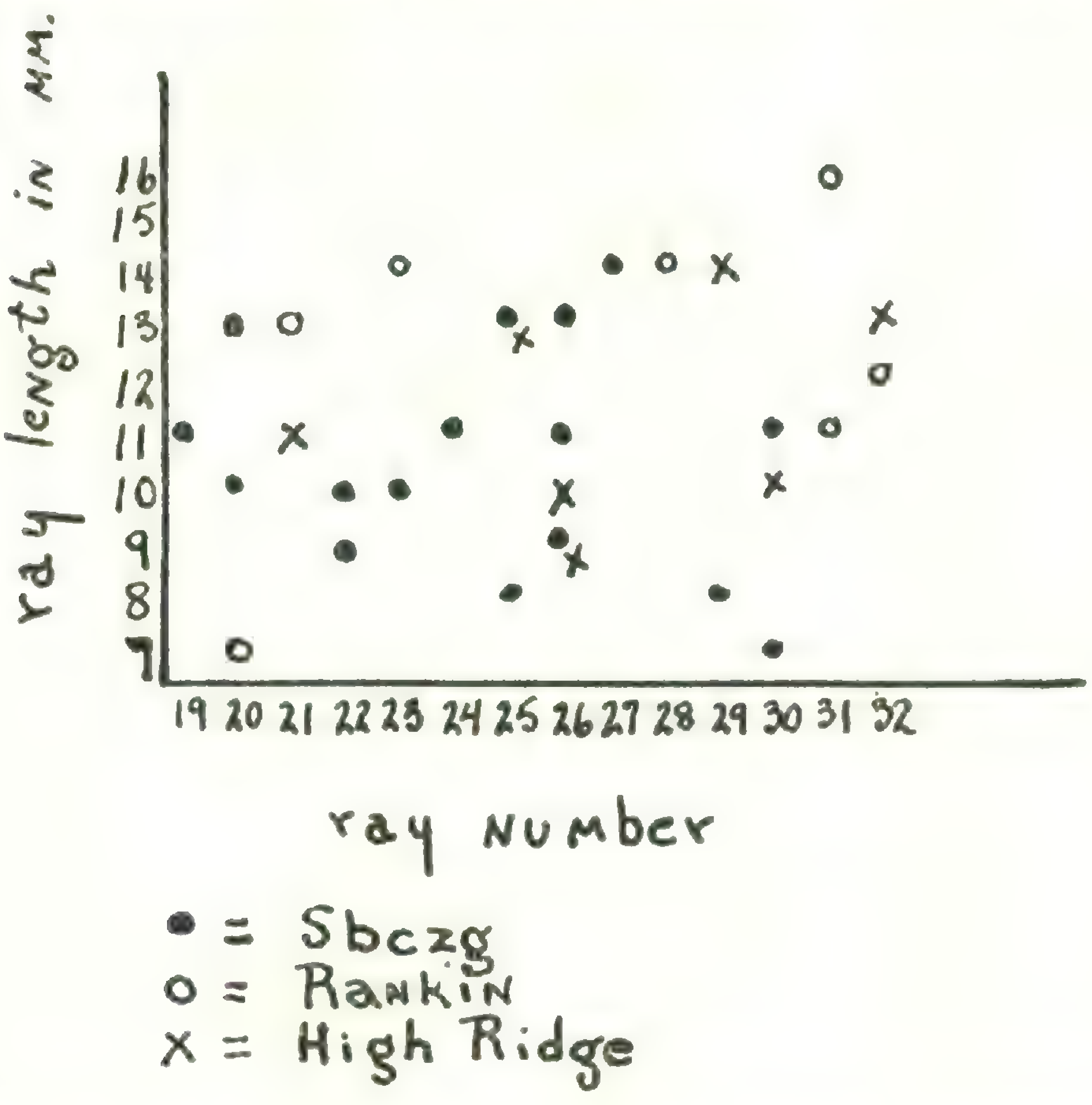


table (table IV) presents these same statistics in another way. While the numbers are too small for precise calculation, it is apparent from mere inspection of the table that there is no very evident association between length of rays and number of rays

(i. e., plants with long rays do not tend to have more rays than plants with short ones, and *vice versa*).

Achenes.—The ripened achenes of *A. anomalus* were found to be highly diagnostic. Specimens from three widely separated localities are illustrated in pl. 4, fig. 2, compared with single specimens of *A. azureus* and *A. turbinellus.* The plate shows how constant are the dark color, the prominent ribs, and the other peculiarities which characterize *A. anomalus.* Achenes from ten to fifteen other species of the genus *Aster* were acquired from herbarium specimens and wild plants. Those of *A. anomalus* were clearly differentiated from all of those examined.

With the achene, therefore, as with the leaf, careful examination revealed characters which would permit of specific determination by that one feature alone.

It was unfortunately not possible to obtain ripened achenes of *A. Shortii.* Immature specimens indicated that they are probably more like *A. anomalus* than any of the other species studied. Seed characters are useful because of their relatively imperishable nature. It is therefore all the more unfortunate that collectors have so entirely neglected fruiting material of the genus *Aster.* The herbarium of the Missouri Botanical Garden is particularly rich in specimens of *A. anomalus,* possessing well over a hundred sheets, only five of which exhibit well-ripened achenes. Collectors should realize that though fruiting material of *Aster* may not make neat-looking specimens, it is nevertheless extremely useful in taxonomic work.

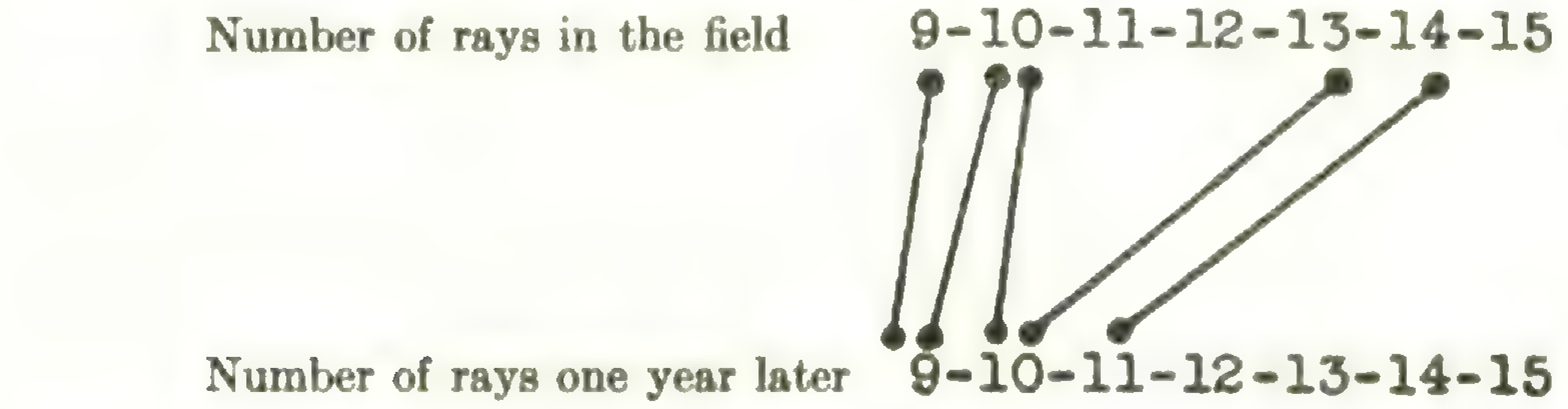
IV. Experimental

Representative individuals from several localities were transplanted to the experimental plot at the Missouri Botanical Garden. Superficially the species was greatly changed by cultivation. The stems were taller, they branched more freely, and the number of flower heads was greatly increased. Plate 4, fig. 5, shows one of the smallest garden-grown plants, and figs. 1 and 3, branches from other individuals. On the other hand, closer examination showed that most individual characteristics persisted, in spite of the changes produced by cultivation. The shape and relative size of the disks and rays remained the same.

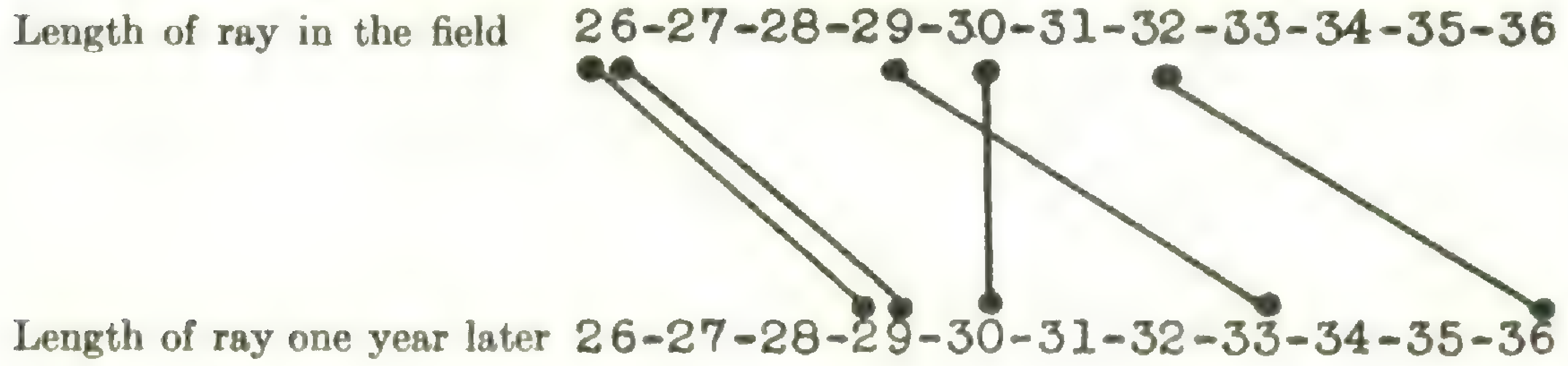
Plants with deeply notched ligules collected at High Ridge, and Rankin, Mo., continued to bear flowers with similarly notched ligules for year after year in the experimental garden. Table v gives exact data on ray number and length for five individuals before and after transplanting. It shows that while the absolute numbers have been somewhat changed, the comparative relations between individuals have remained practically the same.

TABLE V

NUMBER OF RAYS IN FIVE INDIVIDUALS BEFORE AND AFTER TRANSPLANTING—AVERAGES OF FIVE HEADS EACH



LENGTH OF RAY IN MILLIMETERS FOR FIVE INDIVIDUALS BEFORE AND AFTER TRANSPLANTING—AVERAGES OF FIVE HEADS EACH



From these experiments it was concluded that aside from general habit, the differences which exist between individuals in the wild have a strong germinal basis. A further series of experiments was made to determine the genetic relationships between these individual differences. Seeds were collected from five plants growing under natural conditions, three at High Ridge, Mo., and two at Rankin, Mo. The seeds were sown in separate lots and grown as five series of sister (or to be more exact, half-sister) seedlings. Within each group no two plants were alike or even similar; in fact there was almost as great a range of variation in each group of sister seedlings from one mother plant as there was in all the wild plants examined at either High Ridge or Rankin.

Some of the most conspicuous differences between the sixteen

sister seedlings of group Sbczg are tabulated in table VI. The data for number and length of rays are included in tables II and III referred to above. The variation between sister plants is illustrated in pl. 4, fig. 4, where three flower heads from one individual (b, c, f) are contrasted with one each from three sister plants.

TABLE VI

COMPARISON OF SISTER SEEDLINGS, GROWN FROM SEED COLLECTED FROM A SINGLE PLANT

	Ray color	Ray length	Ray number	Ray form	Inflorescence type
Sbczg— 2	Medium	11	30	Irregular	Loose
Sbczg— 3	Medium	10	20	Irregular	Loose
Sbczg— 4	Medium	13	26	Irregular	Very loose
Sbczg— 5	Dark	13	25	Medium	Loose
Sbczg— 6	Medium	14	27	Irregular	Very loose
Sbczg— 7	Light	7	30	Irregular	Compact
Sbczg— 8	Medium	11	26	Irregular	Medium
Sbczg—10	Medium	10	23	Irregular	Loose
Sbczg—11	Light	11	19	Irregular	Compact
Sbczg—12	Light	10	22	Narrow	Medium
Sbczg—13	Medium	9	22	Irregular	Medium
Sbczg—14	Light	11	24	Irregular	Medium
Sbczg—15	Medium	8	29	Medium	Loose
Sbczg—16	Medium	8	25	Irregular	Loose
Sbczg—17	Light	9	26	Irregular	Loose
Sbczg—18	Light	13	20	Irregular	Medium

In the other four groups the morphological relations between sister seedlings were substantially the same. It was therefore concluded that *Aster anomalus* is a highly heterozygous species. In nature it is so often outcrossed that there is no opportunity (as in a self-pollinated species) for the establishment of more or less true-breeding strains within the species. Rather do the differences which characterize individuals combine and recombine anew in every generation, interweaving in precisely the same fashion as do individual characteristics in human families.

V. Summary and Conclusions

1. *Aster anomalus* is a well-differentiated species ranging from central Illinois, through Missouri to adjacent parts of Kansas, Oklahoma and Arkansas.

2. Individual variation, though extremely conspicuous, centers around a "nucleus of common features." Among all the speci-

mens examined and the seedlings grown, there was not one which did not clearly belong to *A. anomalus*.

3. Intensive study of the leaf and the achene revealed characteristics which would make specific identification possible by either feature alone.

4. Transplanting experiments demonstrated that the size and general habit of the individual are largely influenced by the environment. Ray-floret and disk-floret characters, on the other hand, have a strong germinal basis and remain practically unchanged by cultivation.

5. Progeny tests were made of five wild plants from two localities in Missouri. In each of the resulting families of sister seedlings there was a high degree of variation; almost as much as had been found among all the wild plants at either of the localities where seeds were collected. It is concluded that *A. anomalus* is a highly heterozygous species.

Four points related to the problem of species are discussed in the light of these results:

I. Species of the genus *Aster* are notoriously difficult to classify. Dr. Gray, the foremost student of the group, found them very puzzling. We find in his letters (Gray, '93) many references like the following: "I am half dead with Aster. I got on very fairly until I got into the thick of the genus, among what I called Dumosi and Salicifolia. Here I work and work, but make no headway at all. I can't tell what are species and how to define any of them * * * I never was so boggled * * * If you hear of my breaking down utterly, and being sent to an asylum, you may lay it to Aster, which is a slow and fatal poison,"

Wiegand, in his recent report on *Aster lateriflorus* ('28), echoes the same sentiments. It is therefore a point of some theoretic interest that *A. anomalus* should be such an absolutely clear-cut and unmistakable species. It shows that the uncertain speciation found in *Aster* and certain other genera is not necessarily characteristic of the whole genus, but that among a maze of intergrading species there may be some which are well-defined. Or to put it in others words: "Bad" species may have close relatives which are "good" species. This point has a bearing on certain evolu-

tionary theories. At various times and in various ways, the suggestion has been made that whole groups of species may go through "mutating periods," and the genus Aster has sometimes been advanced as one whose species are in a nascent condition. The facts reported above show that here is one species of *Aster* which, though showing unmistakable affinities to other species of the genus, is itself clear-cut and well-defined.

II. Modern genetic research would have us suppose that the differences between species are located in the chromosomes and the other elements of the cell. If this hypothesis is true we would expect to find specific differences expressed throughout the entire organism. The work reported above shows that such is indeed the case in *A. anomalus.* Critical study revealed characteristics which would permit of identification by the leaves or achenes alone. Similar characters could probably have been found for the involucral bracts and for the disk and ray florets. Viewed in the light of these results disputes as to how many characters are necessary for specific delimitation seem rather trivial. Given abundant material it should be possible to find—and even more, to demonstrate—specific differences in all those parts of the plant where germinal differences are not swamped by environmental ones.

III. The fact that a cross-pollinated, continuously outbred species, such as *Aster anomalus,* can still as a whole remain a clear-cut morphological unit, offers serious difficulties to the universal application of the Jordanon, as the writer has already pointed out ('28). The germinal differences between individuals of *A. anomalus* are so many that the chances of finding any two plants which are even phenotypically similar are practically *nil.* If the Jordanon terminology were to be consistently applied it would be necessary to give a name to every individual examined. Clearly in this case, the only practical morphological unit is the whole complex of interweaving individualities which makes up the Linnaean species. Nor is the condition reported here in any sense exceptional. Babcock and Hall ('24), have reported similar conditions for the inheritance of individual differences in *Hemizonia congesta,* and it would be expected that any cross-pollinated species would behave likewise. Since cross-pollina-

tion is more common than self-pollination, the existence of recognizable Jordanons within Linnaean species would seem to be the exception and not the rule.

IV. It is the writer's provisional opinion ('28) that without a high degree of isolation, individual differences are not effective in species forming (among the higher plants at least). The facts reported in this paper lend further support to that hypothesis. *Aster anomalus* would seem to be a species which remains a consistent and independent unit in spite of a high degree of variation between individuals.

VI. Bibliography

Anderson, Edgar ('28). The problem of species in the northern blue flags, Iris versicolor L. and Iris virginica L. Ann. Mo. Bot. Gard. **15**: 241–332. 1928.

Babcock, E. B., and Hall, H. M. ('24). Hemizonia congesta, a genetic, ecologic, and taxonomic study of the hay-field tarweeds. Univ. Calif. Publ. Bot. **13**: 15–100. 1924.

Gray, J. L. ('93). Letters of Asa Gray. pp. 696–697. 1893.

Sinskaya, E. N. ('28). The oleiferous plants and rootcrops of the family Cruciferae. Bull. Appl. Bot. Genet. & Pl. Breed. **19**: 1–648. 1928.

Torrey, J. and Gray, A. ('43). Flora of North America. p. 503. 1841–1843.

Wiegand, K. M. ('28). Aster lateriflorus and some of its relatives. Rhodora **30**: 161–179. 1928.

Explanation of Plate

PLATE 4

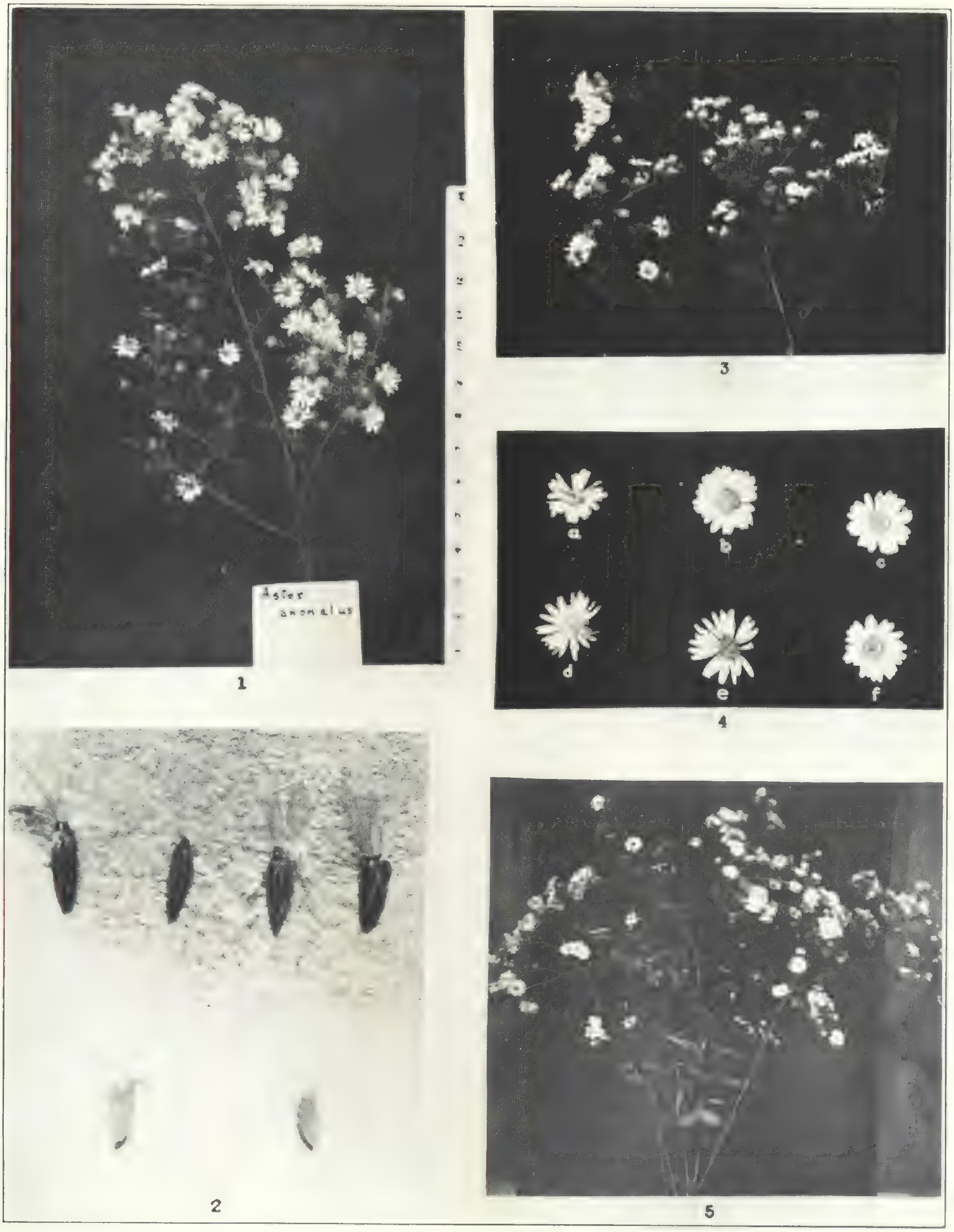
Fig. 1. Flowering branch of garden-grown specimen of *Aster anomalus;* 14-inch rule for comparison.

Fig. 2. Ripened achenes, × 3½. Upper row, *Aster anomalus* from the following four localities, reading from left to right: Rankin, Mo., Van Buren, Mo., St. Louis, Mo., Poteau, Okl.; lower row, *Aster turbinellus* and *Aster azureus*.

Fig. 3. Flowering branches from two garden-grown plants of *Aster anomalus*.

Fig. 4. Flower heads of *Aster anomalus*, × ½: *b, c, f*, three heads from the same plants; *a, d, e*, heads from three other plants.

Fig. 5. Garden-grown plant of *Aster anomalus*.



ANDERSON—VARIATION IN ASTER ANOMALUS

SOME CHEMICAL AND PHYSIOLOGICAL STUDIES ON THE NATURE AND TRANSMISSION OF "INFECTIOUS CHLOROSIS" IN VARIEGATED PLANTS[1]

EVERETT FOGG DAVIS

Assistant Plant Physiologist, Virginia Agricultural Experiment Station
Formerly Instructor in the Henry Shaw School of Botany of Washington University

Introduction

Experiments relating to the phenomena of the contagious nature of certain variegated varieties, when held in graft with a pure green variety of the species, have been known for over two hundred years. The earliest information upon the subject can not be considered reliable for the reason that the observations were recorded by the practical nurserymen, who too frequently failed to consider other possibilities for the appearance of new variegations than their transmission through grafts.

In regard to the contagious nature of the disease, a discussion of the literature must be concerned chiefly with the critical investigations performed by Lindemuth and Baur between the years 1904 and 1908. Very recently, however, Rischkow has attempted to reinvestigate the transmissibility of variegations in certain varieties of *Evonymus japonica.* The recorded experiments and observations of the former two investigators will form the basis for the present discussion of the literature. After considering the results of early investigators in the light of the general advances which have been made in recent years in the study of the mosaic diseases of plants, particularly in the matter of methods and of standardization of technic, the author has repeated certain aspects of these early attempts. From investigations with varieties of *Abutilon* and *Evonymus* new data were obtained which are included in the present paper.

In addition to my efforts to repeat the experiments of Baur, i. e., unsuccessful attempts to induce infection by inoculating

[1] An investigation carried out in part at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

healthy plants with the juices expressed from the leaves of chlorotic individuals and successful attempts to transmit the infection by means of grafts, certain experiments were performed with a view to determine facts concerned with the following:

I. Genesis of the chlorotic areas under the various conditions of light intensity, length of day, and concentration of carbon dioxide, as well as under conditions where the effects of light of different qualities may be observed.

II. Nature of the cellular environment of the green and variegated tissues of leaves held under the conditions mentioned above, determined by employing the following methods:
   a. Histological examinations of living and fixed leaf material.
   b. Determination of hydrogen-ion concentrations by the quin-hydrone electrode and the indicator methods.
   c. Analysis for total acidity by electrometric titrations.

III. Quantitative changes in the pigments and in the chlorophyll a/chlorophyll b and carotin/xanthophyll ratios in varieties infected with contagious variegations.

Discussion of the Literature

Aside from anatomical distinctions, infectious chloroses may be distinguished from non-infectious chloroses by the fact that the causal agency, which for the sake of convenience is commonly referred to as a virus, can be transmitted from a chlorotic (variegated) plant to a green plant. In the case of the non-infectious type the variegations can be perpetuated either by means of inheritance through the seed or by the vegetative reproduction of variegated plant parts. In some infectious chloroses transmission can be readily obtained by the inoculation of infectious plant juices into healthy plants. It has been shown that some species of insects are effective carriers of the virus in the case of certain chloroses. Chloroses which can be transmitted by the inoculation of the infected juice fall into the group of mosaic diseases. Still other chloroses can be transmitted by graft union of chlorotic and green parts, but they have not as yet

been successfully transmitted by inoculation. These have been referred to as "infectious chloroses," and it is to this latter group that the present paper is devoted.

Early Literature.—Historically, the transmission of a leaf variegation to the leaves of a stock or scion has been known since the successful graft experiments performed and reported by Wats in Kensington, 1700, John Lawrence in England, 1715, and Bradley, 1726. Practically, however, this line of research gained impetus in 1868, when a single plant of *Abutilon striatum* Dicks., imported from the East Indies to England, was found to possess a very attractive foliage spotted with green and yellow. Because of its beautiful leaves, an economic demand arose which caused it to be widely reproduced vegetatively in both England and France.

In 1869, Lemoine, in Nancy, made the first observations on the transfer of this leaf variegation to other species of *Abutilon* by grafting. In the course of the same year Morren ('69) wrote:

> "Les expériences [graft transfers] dont nous venons de relater les resultats ont été repetées plusieurs centaines de fois pendant le cours de l'année 1869 par M. Q. Wiot, directeur de l'établissement d'horticulture de Jacob Makoy et Cie, à Liège . . . Elles étâblissent, en effet, cette fois d'une maniere incontestable, la transmissibilité de la panachure du feuillage d'une plante à une autre par une sorte d'inoculation."

Beyond recognizing it as a disease of the so-called "green chromules" transmissible from plant to plant by means of grafting, Masters ('69), Morren ('69), Sageret ('69), Bouché ('71), Lindemuth ('78), and others knew little concerning the true nature or cause of the disorder. As early as 1899, Beijerinck thought it to be like the mosaic of tobacco, and he believed that it belonged in the same class of infectious diseases.

Masters ('69) established the fact that certain species other than the Malvaceae were also capable of transmitting or of receiving similar communicable diseases. He found a white variegated variety of *Jasminum officinale* which transferred its variegated appearance to the green stock, *Jasminum revolutum*. This established a new variety, *Jasminum revolutum foliis aureo variegatis*. Concerning it, Morren reported that if grafted back upon the white variegated variety of *Jasminum officinale*, it would regularly infect it and could thereby produce the variegated characters of "*aureo-variegatis*" upon it.

His work was followed by Bouché ('71), who grafted scions of a yellow and of a white variety of *Evonymus japonica* on the side of the stems of two green specimens. He observed later that these green plants produced twigs which bore clear traces of a whitish venation. He concluded that this change is to be considered as an infection resulting from an interchange of the sap from the white variegated scion. Lindemuth, however, thought it more probable that infection resulted from the scion of the yellow variety instead of the white. Morren ('69) found that infection could be brought about in some cases by introducing a petiole, with a variegated leaf blade attached, into an incision in the bark of the succulent stem of a plant bearing green leaves.

Chief among the early investigators interested in the solution of this problem was Lindemuth, who showed that in the genus *Abutilon* there are species and individuals having varying degrees of susceptibility to the infection. Light was found to favor the development of the mottled chlorosis in the Malvaceae, and high fertility was proved to be an additional factor favoring bright-colored variegations.

It was not until 1904, when Baur began his researches upon the nature of the *Abutilon* infection, that there was advanced a general concept relating the infectious chloroses to the virus diseases such as those of tobacco, potato, sugar cane, aster ("yellows"), and probably likewise the "yellows" of peach.

General Physiology and Pathology of Variegations

Physiology of Non-Contagious Variegations

The fundamental distinctions between non-infectious variegations of the mutant type and infectious variegations of the infectious disease type were recognized by but few of the early authors. Among those who did make this distinction were Vöchting and Lindemuth, although others classed all kinds of variegations in one group.

There have been mentioned in the literature of variegations several ways whereby variegated plants, leaves, shoots, and portions of each may be distinguished in physiological behavior from the clear green counterparts. The studies have had to do

with differences in the content of oxidizing enzymes, water, and turgidity, as well as differences in the concentration of chemical constituents. Where significant chemical differences have been found they compel the botanist to consider the variegated and the green foliage as individuals having very different physiological constitutions.

It has commonly been observed that variegated foliage and diseased plants break the winter rest period before healthy individuals. Lakon ('16, '17), working on the nature of the differences in the yearly periodicity of albino-leaved shoots of *Acer Negundo* L. and *Sambucus nigra* L., assumed with Klebs that this behavior may be accounted for by the inability of such leaves to accumulate and store photosynthetic products during the late summer. These authors believed that persistency in a state of rest, after external factors for growth are favorable, results from an inhibition of the enzymes by an accumulation of the end products for which they are directly responsible. Since in chlorophyll-deficient albino leaves there is no such excess of food reserve during late summer, the following spring finds the enzymes in a position to hydrolyze starches for immediate translocation and consumption. A number of variegated plants have been observed to blossom and fruit more quickly than is customary for the entirely green varieties.

Woods ('99) and Pantanelli ('05) considered that albinism in leaves is a constitutional disease in which the oxidizing enzymes, found always to occur more abundantly in the yellow plant parts than in the green, bring about a primary decomposition of the chlorophyll in certain portions and in certain cells of the leaves.

Pantanelli studied the distribution and the relative abundance of oxidases and peroxidases in the tissues of the variegated and green leaves of *Ulmus campestris* L., *Sambucus nigra* L., and *Acer Negundo* L. He confirmed the earlier results of Woods and further showed that in young leaves oxidases are more abundant than peroxidases, but that in old leaves the reverse relation holds. Pantanelli ('05) and Grandsire ('26) found cells in the chlorotic areas of variegated plants in a higher state of turgidity than in the green. The water content, too, of the light-colored areas is always higher.

In general, variegated varieties are more susceptible to mechanical injury, to fungous attacks, to extremes of temperature, and light intensity than are the green. The leaves, and the entire variegated plant as well, may be dwarfed and may remain sickly and undeveloped,—a further indication that in variegation and albinism we are dealing with a phenomenon which is, from the standpoint of the plant, a constitutional disease.

It is not always the case that the non-infectious types of variegation are inherited through the seed, although as a general rule this is true.

PHYSIOLOGY AND PATHOLOGY OF THE INFECTIOUS VARIEGATIONS

Though the "virus" theories proposed by Baur for infectious chlorosis ('06) have excited but casual interest, many of his experiments, and also those of Lindemuth, have been carried out with painstaking thoroughness. Since these papers have not been widely referred to in the modern literature on the mosaic diseases, it comes well within the scope of the present paper to review those which are especially outstanding.

Our knowledge concerning the nature of the disease and the physiology of infectious chlorotic plants is chiefly the result of the studies made by Baur upon species of *Abutilon*, *Cytisus*, *Evonymus*, *Fraxinus*, *Laburnum*, *Lavatera*, *Ligustrum*, *Ptelea*, and *Sorbus*. Lindemuth, on the other hand, confined his researches to a large number of genera, species, and varieties in the family Malvaceae. Our information in regard to the nature of immunity and susceptibility to infectious variegations among the members of this plant family may be chiefly ascribed to the investigations of Lindemuth. The salient contributions from all the researches in this field will be mentioned under the four major heads, which follow:

INFECTIOUS PROPERTIES OF THE CAUSAL AGENCY

Graft and tissue transplantation experiments.—Lindemuth ('78) and Baur ('04) have shown, as have other investigators before them, that the infectious chlorosis of certain species, particularly some of those belonging to the family Malvaceae, can be readily transmitted from an infected stock or scion either to the green

varieties of the same species or to related susceptible species, by grafting or by the transplantation of living leaf or stem tissue to the wounded surface of a growing stem. Obviously enough, in the latter case, where only living-leaf tissue is used, this transfer of infectious agency must pass quite rapidly out of the infected branch into the susceptible green stock. Careful experiments are still needed to determine the minimum of time which must elapse after a graft union has once been established in order to bring about the first visible evidence that a transfer of the virus[1] from stock to scion or vice versa has been made.

Rischkow ('27a) has given attention recently to the infectious chloroses of *Evonymus japonica,* one of which he described as having the appearance of light yellow stripes along the veins at an early stage in the development of the leaf. The infectious variegation, he states, is associated with the other types of variegations which are non-infectious, such as, for example, the foliage varieties "*marmor,*" "*chlorino-marginata,*" and "*aureo-maculata,*" so that its identity is nearly or entirely masked by them. To establish the existence of the infectious variegation it was necessary for him to graft a plant of *Evonymus japonica* having variegated leaves with one having the uniformly green leaves, so that the chlorosis might be expressed free from all other types.

In all cases it was necessary for a period to elapse, varying in length from one to several months, following the union between stock and scion, before the chlorosis first appeared along the veins of the youngest green leaves. When the grafted parts failed to unite, in no case was the transmission of the variegation acquired. Ageing of the infected leaves was accompanied by a gradual disappearance of the chlorotic stripes along the veins, a change which was frequently accompanied by certain morphological changes which resulted in the formation of chlorotic

[1] The author is aware of no experiments which have been made which can be sufficiently substantiated to warrant the use of the term "virus" without some qualification when it is applied to the causal agency associated with infectious types of variegations. However, for want of a more correct term he is obliged frequently to use it in this paper when reference is made to the causal agency producing "infectious chlorosis." Hereafter the words "virus," "causal agency," and "infectious agency" will be used interchangeably.

areas among the mesophyll cells of the leaf. A criticism which may justly be applied to the conclusions presented in the paper of Rischkow is the fact that they have been drawn from experiments involving single plants.

Inoculation tests.—Baur ('04) made persistent attempts to transmit the variegation by applying juice from the crushed leaves of an infected plant to various species of Malvaceae, but his experiments were always without success. Lindemuth ('07) mentioned earlier unsuccessful attempts of his own and of Lewin to infect susceptible Malvaceae by injecting infecting juices of *A. Thompsonii* into the bark, and by watering the roots of potted plants with the juice from the variegated leaves.

Efforts to inoculate various species and highly susceptible green Malvaceae have been made by cutting and grinding variegated leaves into a pulp which was then pasted over extensive wounded surfaces. Sap has been pressed from spotted leaves and injected, filtered and unfiltered, into sound twigs which were cut off for the purpose and then grafted back upon the mother plants, or these twigs were grown as cuttings. Baur failed to give any statement as to the kind of filter which he used or the methods which were used in applying the filtering process. He completely immersed twigs in a vessel containing expressed juice of infected leaves, and then subjected the vessel to a reduced atmosphere of 20 mm. mercury by using a mercury air pump. The sap was allowed to flow back into the intercellular spaces under normal air pressure. Of the pieces that survived this treatment, some were rooted as cuttings while others were grafted back upon the parent stock. These experiments all gave negative results. To date no experiments have been recorded that show a transfer of the variegation except when two plant parts, one variegated (diseased), the other green (susceptible), are placed in close contact, so that the living cells of one are in intimate relation with the living cells of the other.

Attempts at transmission by insects.—Rischkow ('27b) conducted an experiment with a view to determining whether insects feeding on *Evonymus japonica* infected with chlorosis could transmit the causal agency to healthy plants. He kept the red spider, *Tetranychus telarius*, feeding and reproducing in large

numbers on the foliage of two plants placed adjacently, one infected with chlorosis, the other normal green. The experiment lasted for four months but no transfer of the infectious chlorosis was obtained.

The causal agency in relation to plant organs.—Various organs of the susceptible plants behaved differently as regards the infectious properties of the causal agency.

Root.—For the roots Baur ('04) wrote, "Ich verbrachte dann ferner ausgetopfte gesunde Pflanzen für Stunden und Tage mit ihren Würzeln in den unfiltrierten Presssaft aus kranken Blättern, alles mit demselben negativen Erfölge." However, Lindemuth ('07) obtained repeated infection through the root of *Althaea rosea* (L.) Cav. by grafting the entire plant high upon the stem of *Abutilon Thompsonii*. There were variegated leaves left below the graft. In this case there was established a union between the fleshy perennial root and the cambium of the stem.

Stem.—Baur concluded from certain observations from crude experiments that the virus travels very slowly through the phloem region of the stem. This conclusion is, however, not especially well founded as is obvious from the following description of his experiment. Ringing experiments were performed to determine whether or not the virus travels through the xylem or phloem regions of the stem. Plants of *A. avicennae* Gaertn. were ringed for a width of 0.5 cm. and a shoot of *A. Thompsonii* was grafted in some experiments below and in others above the ringing. The experiment was carried on three times, once with the graft above and twice with the graft below the girdling. In the first case, the plant *A. avicennae* was infected at the tip after an interval of two weeks. It developed three small stunted leaves and died four weeks after the operation. The stock below the ringing developed two dormant axillary buds before the death of the tops above the girdle. These buds produced two strong shoots during the course of the summer. Both shoots remained green-leaved. In the other two cases the grafted shoot of *A. Thompsonii* likewise grew well, living in union with the stock twelve weeks before the experiment ended.

As far as is known, the stem is not in any way visibly affected by the disease. If Baur is correct in his assumption that the

phloem alone carries the infectious ingredients, it would be of interest to study the vascular strands in stem and in leaf tissues for any structural modifications which might be the results of chlorosis infection.

Another point of interest in connection with a discussion of the infectious properties of the causal agent in relation to the stem has been pointed out by Baur. He reached the conclusion from experiments with certain species of *Abutilon* that the active agency can be carried from an infected stock through a healthy scion. In its turn the healthy scion may infect the healthy scion of a susceptible species grafted upon it without itself succumbing either to the infection from below, or, as would be the case later, from the infected scion above. The experiment will be described under the heading "immunity" which is to follow.

Leaves.—Depending upon the stage of development, leaves, as in the unexpanded buds or in the expanded leaf blades, appear to exhibit distinct peculiarities toward the infectious agency. A description of typical experiments will show these relationships as Baur considered them to be true.

On strongly variegated specimens of *Abutilon Thompsonii* Baur grafted scions of a green-leaved variety of *A. arboreum* which is susceptible to infectious chlorosis. On a portion of these the leaves on the *A. Thompsonii* stock were left attached, and on another portion the leaves on the stock were removed and no new leaves were allowed to develop. On the latter the scions all remained green, on the former they became variegated. Some time later, an axillary bud was allowed to give rise to a variegated shoot upon a stock of the previous experiment on which the leaves had been removed and the scion of which had consequently remained green-leaved. Three weeks after the first variegated leaves had appeared on this shoot, the scions developed variegated leaves.

Buds which are formed while the plant is variegated will develop later into variegated leafy shoots and will infect the plant even if, in the meantime, the plant has become completely green-leaved through proper light treatment. Buds which will later produce variegated leaves have no power to infect while

they are present in the dormant condition. Where buds from an infected plant are transplanted to a susceptible green-leaved plant, infection takes place more rapidly and in a larger percentage of cases where the variegated leaf of the bud is also transplanted.

Leaves which are in the process of expanding from the closed-bud stage are seen to require a period of development, or enlargement, before they can be observed to possess mottling either under reflected or transmitted light. At this stage they seem to be well supplied with chlorophyll.

Baur believed that he had proved by experiment that these light-colored spots are centers for both the reproduction and the infection of the virus. Along with the increase in size, a leaf which has become variegated can probably bring about infection in still younger leaves, so that the infection spreads, always in the vicinity of the actively growing tips. Leaves which are already mature and uniformly green when the infection spreads will remain so.

Seed and stem.—It seems to be a general observation that those variegations which have proved to be infectious chloroses are not usually transmitted through the seed from the infected parent stock. However, there are many examples which have not yet been tested adequately.

In this connection an experiment of Lindemuth ('07) may be mentioned. Of ten seedlings that grew from seeds of *Lavatera arborea* L. infected with *Abutilon Thompsonii* variegation, one became variegated at once, three became variegated later but eventually lost the variegation entirely, while six grew green-leaved from seed. In the case of the horticultural variety of *Abutilon*, "H. Cannell," the infected plant produced seed from which there were grown twenty seedlings, three being variegated. Lindemuth reported that further details connected with the ancestry of the seed were lacking. He was inclined to believe the variegated seedlings arose spontaneously.

Baur advanced the hypothesis that in developing leaves the virus accumulated, by drawing from the general supply in the stem, only when the leaves had developed so far as to provide for a material interchange of food products in the direction of

the stem and vice versa. Upon this assumption it is only necessary to argue that in the embryos of seeds the potential leaf organs have not yet reached this stage in their development, and that without an accumulation of the virus from the stem there is too little present in the seeds to bring about infection.

That the virus exists in such small amounts in the stem of a variegated plant has been assumed from the fact that a plant can be cured by removing all the leaves for two successive crops. The third crop of leaves to appear will be pure green. In other words, by this procedure it has been shown, according to Baur, that there is only a limited amount of virus located in the stems, and that this supply has been exhausted after the first two crops of leaves have been infected and subsequently removed.

Floral parts.—There are many observations to show that variegation also occurs in the tissues of floral parts. Some variegations have been known to occur on plants infected with chloroses and probably result from the infection, while others, such as the yellow stripes on fruits of apple and pear, occur on non-infected plants, a fact which makes their pathogenicity seem doubtful.

In certain infected Malvaceae the leaves, ovary (including the carpels), as well as the young bark, may all show variegation, as, for example, *Althaea rosea* (L.) Cav. infected with the virus from *Abutilon Thompsonii* fruiting with variegated seed pods.

RELATION TO SOME EXTERNAL FACTORS

The infectious character of this disease bears a very direct relation to the presence of light. Here again Baur's work remains our chief source of knowledge in regard to the relation between the variegated properties of the disease types and certain of the external environmental factors.

From the earliest attempts to investigate the nature of the disease, it was found that the mosaic pattern of some variegated leaves held a close relationship to the intensity of sunlight. Lindemuth was the first to observe that variegated Malvaceae hold their characteristic mottling only so long as they are given a sufficiently high intensity of sunlight.

Light intensity experiments.—An extreme case was that in

which it was claimed by Baur that shielding the old variegated leaves from light was all that was necessary to inhibit what might be either the production or the translocation of the virus so that all new leaves developing at the vegetative growing points became and remained pure green, whether they were exposed to full sunlight or not.

It was also reported that by keeping the newly developing leaves in darkness for a time, infection was not hindered. The findings of Lindemuth were confirmed, and it was shown that strongly variegated plants could be made to lose the variegated appearance if placed for a time in sunlight of low intensity, whether they were allowed to remain in deep shade or given a small fraction of the direct sunlight for only a portion of the day. Baur's experiments were, however, of the crudest sort. The yellow spots on the newly developing leaves were said to become smaller and sparser until the leaves showed isolated yellow flecks and in the course of time became pure green. In the younger leaves the greening proceeded most rapidly, while older leaves in which the variegation formed under the better source of light remained for a long time without noticeable change. Where the old leaves were removed the greening of the entire plant was said to go on more rapidly. This is, however, a difficult point to verify. From these facts the following conclusions have been reached. The quantity of virus formed in a spotted plant is dependent, first, on the light intensity, and second, on the size of the yellow spots in the leaves.

Quality of light.—To a certain extent, experiments with blue-green and red light gave similar results. The plants remained spotted in both glass houses but clearly less in the blue than in the red.

Inasmuch as the plants under this treatment were placed in a position where they remained in the shade for a half of the afternoon, it is doubtful whether the results which Baur obtained can be attributed to the quality of light. What makes his interpretation even more unlikely is the additional fact that the intensity of light would be materially reduced under colored glass and especially under blue glass. The experiment shows, however, that the mottled condition can be produced under light in both halves of the spectrum.

Carbon dioxide.—The question which Baur raised, "Is the virus production connected in some way with the carbon dioxide assimilation process?" remains unanswered. The obvious experiment of growing variegated plants for a long time in carbon dioxide-free air was tried, but failed because the experimental plants became defoliated after a few days.

Soil and mineral nutrients.—Future experiments will undoubtedly determine to what extent, if any, fertilizers and soil factors can be taken into consideration in the production or inhibition of the mottled condition of the leaves. This phase of the problem did not receive much attention by the earlier workers. A single statement by Lindemuth, to the effect that soils high in fertility did favor a strong infection may doubtless stimulate future investigations along this line.

Climatic factors.—Lindemuth has shown that several shrub-like Malvaceae, such as *Althaea rosea* (L.) Cav., when infected, remained so during the vegetative period but lost the variegation during the course of the winter rest period. Other shrubs, for example, *Kitaibelia vitifolia* Willd., were said to retain the infectious chlorosis over the winter and for the remainder of life, in the stalks, leaf buds, or basal green leaves.

HOST RELATIONS

The relation of host to the mosaic patterns in the leaves.—The manner in which the infectious chlorosis was expressed in the various species differed considerably. In *Abutilon arboreum* only large single yellow spots appeared to interrupt the uniformity of the green; in other species, for example, *A. Sellowianum* Reg., the surface of the leaf exhibited a mosaic type of combination of clear green, clear yellow, and yellow-green fields in all possible gradations. In still other species, for example, *A. indicum* (L.) Don, the whole leaf became yellow or white except for a few small green spots, and remained small and wrinkled.

In the foliage varieties of *Ligustrum vulgare* an infectious type had been isolated which was present and obscured by a non-infectious variegation. It was said that if care were taken contagious symptoms might be recognized on young leaves by the yellowing along the veins. There appeared only an incon-

spicuous yellowing of the leaves on species of *Laburnum* carrying the infection. The sharply defined variegated spots or stripes were missing. In the particular case of *Sorbus Aucuparia,* the infectious variegation was further modified so that only the tips of the teeth on the margin of green leaves were chlorotic-yellow.

Limits of susceptibility and of immunity to the virus.—Lindemuth ('78, '99a, '99b, '02a, '02b, '07) has given special attention to the extent to which different members of the Malvaceae are susceptible. His first paper appeared in Berlin in 1870. A very excellent review of all of his investigations and a comprehensive discussion of the literature is included in his 1907 paper. Different species of Malvaceae were shown to differ markedly in their ability to withstand and to take the infection. The author of the present paper has arranged the infectious species referred to in the literature in a table which accompanies this discussion. Footnotes refer to the relative degree of susceptibility or to the type of resistance found.

Abutilon indicum and *Sida Abutilon* show a type of variegation consisting of a single more or less expanded yellow spot in the leaf with little of the green remaining. Such plants are so severely infected that they frequently die because of the inhibited carbon-dioxide assimilation. According to Lindemuth ('07), resistance and immunity may depend upon the individual characteristics of the plant, upon the season, or upon the methods which are used in making the graft and transplantation. These points are illustrated in Lindemuth's experiments with *Abutilon arboreum.* He used *A. arboreum* four times as a scion upon *Abutilon Thompsonii* and twice as a stock for *A. Thompsonii* scions. Of this number, *A. arboreum* was infected three times as a scion and once as a stock. Old plants did not take the infection readily if at all. At times as many as twenty grafts were made between certain susceptible green and infectious chlorotic individuals, with the result that none became infected. At other times he was able to infect three out of every five plants. *Lavatera arborea* L. has been considered by some to be immune, yet Lindemuth was able to show, by using large numbers of individuals at different times, that its range of susceptibility varied all the way from immunity to a super-susceptibility.

Interesting experiments have been performed by Baur in this general connection. Scions of an immune strain of *A. arboreum* were grafted on several strongly variegated plants of *A. Thompsonii.* The scions remained pure green. On part of these *A. arboreum* scions were grafted shoots of highly susceptible *A. indicum* stock. Within a short time these superiorly placed scions of *A. indicum* became variegated, although the subsequently formed leaves of the *A. arboreum* scions never became yellow-spotted. The conclusion was drawn that the virus was carried up through the *A. arboreum* scion which was immune to it, and entered the topped-graft scion of *A. indicum* without becoming in any way inactivated in the course of the process. However, scions of *A. arboreum* which were held for a time in union with a variegated stock of *A. Thompsonii* and later removed and grafted upon a highly susceptible stock of *A. striatum* never succeeded in transmitting the variegation to the susceptible *A. striatum* stock. The assumption was made as a result of this experiment that the virus did not reproduce itself while in the latent condition in the stem of the immune *A. arboreum.*

In another instance, an immune strain of *Abutilon striatum* Dicks. was established through the spontaneous development of two pure green shoots on a strongly variegated plant of *A. striatum.* These were eventually removed and propagated as cuttings. All of these individuals remained immune to infectious chlorosis in spite of attempts to infect them by grafting the latter upon other chlorotic Malvaceae. It was not discovered whether this immunity carried itself through the seed or not.

Characteristic immunity in Malvaceous plants may be of three types, according to the assumptions of Baur: (1) The non-infected parts of plants may show immunity by preventing the passage of the virus into such parts. (2) After entering the previously non-infected parts the virus may be subsequently rendered inactive. (3) The virus may gain entrance into the non-infected parts, and then in some way it may be possible for the "infected" plant to remain indifferent to the virus without destroying the infectious character of the latter. On the other hand, Lindemuth chose to consider experimentally the

immunity for each individual before he would believe in any one type of immunity which could be applied to a whole group of plants.

Distribution of the causal agency among plants.—There have been reported within the last two hundred years large numbers of isolated cases where variegations have been said to result from stock and scion infection. However, few observations have met the approval of scientific investigators for the reason that they have been largely described by laymen who have little or no insight into other possibilities in connection with their appearance. With so many variegations in horticultural establishments which answer the general description of the infectious types, there is still a necessity for extensive and reliable studies to be made in spite of the extent to which the initial efforts of Baur and Lindemuth have contributed.

There are frequently found in recent horticultural literature references to new forms of variegated varieties appearing spontaneously outside of cultivation among the wild plants. It is exceedingly likely that in certain cases the causal agency of infectious chlorosis is responsible for the sudden appearance and the spread of these within the limits of localized areas.

Until some direct or indirect method can be found to carry the virus to unrelated plants other than by grafting, the investigator seeking to establish the communicability of infectious chlorosis to other species is seriously handicapped. Relatively few grafts are congenial when carried on outside of closely related varieties and neighboring species. Table I furnishes a fair approximation of the extent to which infectious chlorosis has been transferred between members belonging to the plant families Caprifoliaceae, Celastraceae, Cornaceae, Leguminosae, Malvaceae, Oleaceae, Rosaceae, and Rutaceae. Other families, the genera of which have been suggested as having possible relations to types of infectious chlorosis, are Euphorbiaceae and Nyctaginaceae.

Summarizing the information, the following points require emphasis: (1) The manner in which the infectious chlorosis is expressed in the various species differs considerably; thus, variegations may be recognized easily or with relative difficulty.

TABLE I

HOST RANGE OF INFECTIOUS CHLOROSIS

Source of the virus	Host recipient	Variegation transmitted through				Authority
		Graft	Bud	Tissue	Seed	
Abutilon striatum Dicks. var. *Thompsonii* Veitch.	*Abutilon* var. Africain	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. arboreum* Sweet*	±	–		–	Baur, Lindemuth, Morren
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. *atrosanguineum*	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. Avicennae* Gaertn	++	–		–	Baur, Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Cannell	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. Darwinii* Hook	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. Darwinii* var. *tessellatum* Hort.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Erfurter Glocke	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. esculentum* St. Hil	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Feuerball	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Firefly	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Wilh. Heuer	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. hybridum* var. *grandiflorum* Hort.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. inaequale*	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. indicum* Sweet	++	–		–	Baur, Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. insigne* Planch	±	–			Morren, Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Karl Schweizer	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Lemoine	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Martins	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. megapotamicum* St. Hil. & Naud	+	–		–	Baur, Lindemuth, Morren
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. *Patersoni*	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Reve d'Or	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Royal Scarlet	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. *Savitzii* (tricolor)	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Schneerose	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. Sellowianum* Regel	++	–		–	Baur, Lindemuth

TABLE I—*Continued*

Source of the virus	Host recipient	Variegation transmitted through				Authority
		Graft	Bud	Tissue	Seed	
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Souvenir d'Arago	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Souvenir de Bonn (tricolor)	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Souvenir de Kotschyi Hochst	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. spec. 234	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. *striatiflorum*	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. striatum* Dicks.	++	–		–	Baur, Lindemuth, Morren
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. *sulphureum*	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. venosum* Lem.	+	–		–	Baur, Lindemuth, Morren
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. vitifolium* Presl	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A.* var. Philippine Welser	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Althaea ficifolia* Cav	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. officinalis* L.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*A. rosea* Cav.	+	–		–	Baur
A. striatum Dicks. var. *Thompsonii* Veitch.	*Kitaibelia vitifolia* Willd.**	±	–		–	Baur, Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Lavatera arborea* L.	±	–		–	Baur, Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Malva sylvestris* L. var. *mauritiana* Mill.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*M. verticillata* L.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Malvastrum capense* Garcke	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Modiola decumbens* G. Don	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Sida mollis* Herb.	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	S. *Napaea* Cav	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Sidalcea candida* A. Gray	+				Lindemuth
A. striatum Dicks. var. *Thompsonii* Veitch.	*Anoda hastata* Cav	+			–	Lindemuth
Cornus alba L.	On others	–				
Cornus alba var. *argenteo variegatum elegans* Hort.	*Cornus alba*	–				Baur, others
Evonymus japonica L. var. *argenteo marginatus*	*Evonymus japonica*	–			–	Baur, Bouché
E. japonica L. var. *aureo-marginata* Hort.	*Evonymus japonica*	+				Baur

TABLE I—*Continued*

Source of the virus	Host recipient	Variegation transmitted through				Authority
		Graft	Bud	Tissue	Seed	
E. japonica var. *marmor*	*Evonymus japonica* var. *chlorino-marginata*	+				Rischkow
E. japonica var. *marmor*	*E. japonica* var. *aureo-maculata*	+				Rischkow
E. japonica var. *marmor*	*E. radicans* var. *marmor*	+				Rischkow
Fraxinus pubescens Lam. var. *aucubaefolia* Hort.	*Fraxinus* spp.	+				Baur
Jasminum officinale L. var. *variegata* Hort.	*Jasminum revolutum* Sims		+			Masters, Morren
J. revolutum Sims. var. *aureo-variegata*	*Jasminum officinale*	+				Masters, Morren
Laburnum vulgare Griseb. var. *chrysophyllum* Spath.	*Laburnum alpinum* Griseb.	−				Baur
L. vulgare Griseb. var. *chrysophyllum* Spath.	*Cytisus hirsutus* var. *chrysophyllum* Reiser		+			Baur
L. vulgare Griseb. var. *chrysophyllum* Spath.	*C.* var. *purpurens*	−				Baur
L. vulgare Griseb. var. *chrysophyllum* Spath.	*Laburnum vulgare* L.	+				Baur
L. vulgare var. *aurens* Hort.	*Laburnum vulgare** ‡	+	+	+		Baur
Ligustrum vulgare L. var. *aureum* Hort.	*Ligustrum vulgare*	−				Baur
L. vulgare var. *aureo-variegatum* Spath.	*Ligustrum vulgare*	+	+		−	Baur
L. vulgare glaucum var. *albo-marginatum* Spath.	*L. vulgare*	−			+	Baur
L. vulgare var. *aureo-variegatum* Hort.	*L. vulgare* var. *aureum*	+			±	Baur
Ptelea trifoliata L. var. *aurea* Hort.	*Ptelea trifoliata*	−	−	−	+	Baur
P. trifoliata var. *variegatum*	*P. trifoliata*	+				Baur
Sorbus Aucuparia L. var. *Dirkenii aurea*	*Sorbus Aucuparia*	−				Baur
S. Aucuparia L. var. *lenteo-variegatum*	*S. Aucuparia*		+			Baur

* An immunity which permits the virus to pass through the stem with unaffected infectious properties.
** An immunity specific with certain individual specimens.
\+ In all cases transmissible.
− In no case transmissible.
± Transmissible in some instances, not so in others.
++ Very strongly susceptible.
‡ Susceptible to the transplantation of cortex tissue from the infected stem.

(2) Infectious chlorotic variegations are usually of the typical *aurea* (yellow) type. (3) Strongly variegated plants may send out green shoots which appear immune to infection. (4) Immune stems are said to carry the disease unaltered while the exact nature of individual immunity and susceptibility remains unknown. (5) A "variegation" may sometimes consist of an infectious chlorotic type in combination with a non-infectious type, in which case the former may be completely masked by the presence of the latter. (6) Infectious chlorosis is known to occur among eight plant families, eighteen genera, and roughly among thirty-five species.

NATURE OF THE CAUSAL AGENCY (A TRANSMISSIBLE TOXIN THEORY)

As a result of his studies, Baur ('06) postulated a toxin "virus" theory and stoutly opposed every suggestion that the infectious agency might be associated with a living entity of submicroscopical size. Nor did he concede the probability that species of *Abutilon* in tropical habitats become regularly infected with the infectious chlorosis agency through an intermediate and native insect carrier. He believed it more likely that the observed spontaneous spread of the variegation in the East Indies was due rather to its propagation by the inhabitants for ornamental purposes.

It is difficult to see how a critical examination of the evidence used by Baur to advance a toxin "virus" theory will permit any one to speculate very directly on the probable nature of the infectious agency. Certainly, in view of the modern knowledge and opinions in regard to the transmissibility and physiology of virus diseases of both plants and animals, such facts as those enumerated below appear entirely inadequate. Baur ('06b) has presented these facts in the support of the assumption that the causal agency for infectious chlorosis is not an organism.

"Ich will trotzdem auf einige Ergebnisse der eben geschilderten Versuche kurz hinweisen, die mit der Annahme eines parasitären Organismus nicht gut vereinbar sind. Hierher gehört zunächst die absolute Abhängigkeit der Infizierung vom Lichte . . . Ferner die Tatsache, dass das Virus durch den Transpirationsstrom nicht geleitet wird, sondern, wie die Ringelungsversuche wenigstens sehr wahrscheinlich machen, nur in den Geweben, die der Leitung der plastischen Stoffe dienen. Drittens endlich der Umstand, dass das Virus, bei der Entstehung infizierter Blätter verbraucht, gebunden wird. Aus den

Versuchen folgt ja dass das Virus, das zu einem gewissen Zeitpunkte in einer Pflanze vorhanden ist, sich in den in einem gewissen Entwickelungsstadium befindlichen Blättern restlos ansammelt und hier festgelegt wird."

It is said that Beijerinck ('99), who saw the exhibit of Lindemuth's grafted Malvaceae, considered the chloroses in the same class of infectious diseases as the mosaic of tobacco. Baur ('06) has referred to the virus of tobacco mosaic as perhaps being more stable a virus than the "virus" of *Abutilon* chlorosis. To him the causal agency appears as a highly organized chemical substance which behaves as a toxin; differing, however, from other toxins in that it is synthesized directly in the infected cells after the manner of an autocatalytic chemical reaction. Lindemuth ('07), however, said little in regard to the nature of the infective agency but preferred to look upon it as possessing life and the power of reproduction.

Anatomy of Leaf Variegations

The recent investigations of Funaoka ('24), Tsinen ('23, '24), Hein ('26), Smith ('26), and Küster ('27) have materially advanced our knowledge upon the anatomy, histology, cytology, and pathology of non-contagious variegations. The paper by Küster referred to above is a monographic treatment of the literature and cites 159 references of which 42 have been published during the last five years. It is not intended here to do more than reiterate a few of the outstanding facts in regard to the anatomy of variegations.

Küster ('27) arbitrarily divided all variegations into two classes: variegations in which the limitation of the chlorotic areas appear irregular, and variegations with sharply limited chlorotic areas. He stated that it is to the former class that all or most pathological or infectious variegations belong.

Smith ('26) has observed in the chlorotic mesophyll cells of living and fixed sections of *Evonymus japonica* vars. "*medio-picta*" and "*argenteo-variegata*," "vacuolate bodies comparable to those found in tobacco and petunia mosaics." However, it is an error to state that both of these varieties were studied by Baur. To the knowledge of the present writer the former of these variegations has not been mentioned in any of Baur's

work. While the "*argenteo-variegata*" type is mentioned, it is probable, from Baur's remarks, that it is not to be considered infectious:

> "Die erstere Varietät ist nicht infektiös, ich habe eine grosse Anzahl von Pfropfungen von grünen auf weissrandige und von weissrandigen auf grüne Pflanzen mehrere Jahre hindurch beobachtet."

These recent observations by Smith appear significant when it is remembered that the occurrence of vacuolate bodies is being used by some plant pathologists and plant cytologists working on the nature of the mosaic diseases as a criterion for the presence of the infectious virus. Should it become a well-established fact that such intracellular bodies are widely distributed among variegated phenomena, the present interpretation of their presence in the cells of tobacco plants affected with the mosaic disease will need revision. In the meantime every effort should be made to determine whether a contagious variegation exists in these varieties of *Evonymus.* The reader is referred to the recent publication of Rischkow ('27b) and to the author's experiments which are described in this paper as having some significance in this connection.

As a possible explanation for the occurrence of vacuolate bodies in variegated plants where the transmissibility of variegations has been doubted, is the view, taken by some, that the presence of a striking leaf pattern of a non-infectious type of variegation may obscure the existence of a faintly expressed type of infectious variegation associated with the former in the foliage leaves. It has been shown, in the case of *Evonymus japonica* and *Ligustrum vulgare,* that in some instances where the infectious and the non-infectious types occur together, they can be separated by grafting the variegated upon the green variety. By this procedure the transmissible type may then infect and cause the variegation to appear in the tissues of the green leaves. The possibility exists that if such an infection could be brought about experimentally in the case of *Evonymus japonica* vars. "*medio-picta*" and "*argenteo-variegata,*" there might be found in the mesophyll cells of the infected plants vacuolate bodies comparable to those already found by Miss Smith. Such a discovery would justify her conclusion, namely, "the vacuolate bodies, therefore,

have been observed as yet only associated with the infectious chloroses." Until work is done which proves that the material described by Smith contained an infectious variegation associated with the non-infectious varieties "*medio-picta*" and "*argenteo-variegata*," it can be concluded that vacuolate bodies typical of those found in cells infected with mosaic disease of tobacco have been found in the chlorotic cells of a variegation which is infected with neither infectious chlorosis nor mosaic diseases.

As a result of his cytological studies upon *Evonymus japonica* varieties infected with chloroses, Rischkow ('27b), who was plainly unaware of the findings of Miss Smith, has reached the conclusion that the "infectious chlorosis" and the mosaic diseases can be distinguished from each other chiefly by the absence of the X bodies from the cells of leaves infected with chlorosis. The data from his cytological studies can be criticized, first, because the samples were taken from single plants, and second, that a statement of the cytological methods which were used is not included. Since it is well known that X bodies found in the leaves of tobacco diseased with mosaic are soluble in some killing fluids while insoluble in others, it is difficult to understand why Rischkow should have neglected to mention the killing fluid which was used in the preparation of his stained sections.

One of the chief contributions made by Rischkow on the cytology of infectious chlorosis in *Evonymus* results from the fact that he describes transparent pustules which arise upon the under side of the leaves and project from the lower surface for a distance not greater than 90–100 μ. The author states that large numbers of these pustules are present when a plant is infected with contagious variegation, although very few if any can be found upon the leaves of a healthy plant. By sectioning, it can be shown that they originate through the hypertrophy of groups of single cells in the mesophyll. Typically, the intumescences are enlarged cells rich in water and with more or less decolorized chloroplasts. As the leaves of normal plants change from green to chlorotic as the result of infectious grafts it is said that the number of intumescences is increased along the lateral veins of young leaves at a rate which permits them to keep abreast the development of the chlorotic stripes.

Bouché ('71) observed a variegation, proved by him to be infectious upon *Evonymus japonica,* which could be seen only with difficulty in old leaves but more easily in young leaves. He believed this was because it followed only the conductive strands of the leaf. Although Rischkow ('27b) failed to mention the work of Bouché, it would appear probable from the descriptions of his variegation that his "geadertepanaschierung" is the same type of infectious variegation as that of Bouché.

For the infectious Malvaceae, Küster touched briefly upon the fact that the richly sprinkled pale and green areas are polygonal, for the reason that the conductive strands of the netted system very frequently become the limits of the pale and green fields. Differentiations of the tissues and cells were discussed. In cross-sections of some tissues the thickness of the pale portion was the same as the green. In others there were striking differences which expressed the inhibition of tissue formation in the light-colored leaf areas.

The cytology of plants infected with this type of chlorosis needs to be worked out carefully for various environmental conditions. The bleaching and the metamorphosis of chloroplasts need to be studied in connection with environmental influences. The true nature of the vacuolate bodies of Smith ('26) needs also to be studied.

Hein ('26) and Smith ('26) described the degeneration of chloroplasts in living and fixed material for a number of non-infectious leaf variegations.

Chemistry of Variegations

PIGMENTS

Aside from the obvious deficiency of chlorophyll pigments in the pale areas of all variegated leaves, it is of interest to note that in general, and possibly with but very few known exceptions, the virus causes a yellow instead of a white, brown, red, or other colored leaf character to appear. Whether a greater production of carotinoid pigments accompanies the infectious disease has not as yet been satisfactorily determined. It may be that the yellow color will be simply explained by the reduction in the amount of chlorophyll so that the other leaf pigments are no longer masked by the dark green pigment.

The concentrations and the relationships of flavones and anthocyanin pigments to variegated species have received no attention.

It would be of interest to know whether the normal ratio of chlorophyll a/chlorophyll b and of carotin/xanthophyll remains the same in infected varieties as they are in the green varieties. In the non-infectious variegated *Coleus*, var. "Golden Bedder," Schertz ('21) found great deficiency of a and b chlorophylls and more xanthophyll and more carotin than in the green.

CARBON DIOXIDE ASSIMILATION PRODUCTS

Schertz ('21) found starch present, especially in the guard cells of mottled leaves and other places in the chlorotic area, sufficient to give a good test with iodine. Studies on the total carbohydrate content and its periodic fluctuations showed that photosynthetic activity in the mottled leaves was greatly reduced. Grandsire ('26) has shown that in the albino leaves of *Hemerocallis*, *Acer*, *Cornus*, and *Spiraea* there is as great a variety of carbohydrates as there is in the green, but they are notably lower in absolute amounts. Starch, however, is regularly absent.

NUTRIENT RELATIONS: ASH, INORGANIC SALTS

All investigators seem agreed that there is a higher ash content in the variegated portions of leaves than in the green. In organic matter the opposite is true. From his analyses, Grandsire ('26) showed that albino leaves of the genera mentioned were poor in calcium and rich in potassium. Phosphorus was present in equal proportions in the green and white leaves at the beginning of growth but diminished with age, a condition which was more marked in the white. The ash of white leaves was distinguished from the green in that it had a higher percentage of soluble phosphorous pentoxide. The quantities of other ash constituents, such as iron, magnesium, and sulphur, differed only slightly in amount.

METABOLIC ACTIVITY

Osmotic pressure.—It is generally recognized that pale areas and albino leaves are higher in water content, as well as in the osmotic pressures of the cells. Pantanelli ('05) has made the

suggestion that the latter fact may be due to the presence of metabolic constituents of low molecular weight.

Nitrogen.—Variegated leaves are especially characterized by richness in soluble nitrogen and by a deficiency in total and nitrate nitrogen (Schertz, '21, and Grandsire, '26). Grandsire reported a steadily diminishing supply of total nitrogen, in both the green and in the albino leaves which he studied, as growth continued. However, total nitrogen losses in the variegated leaves were much more rapid than in the green. Insoluble nitrogen, whether referred to by dry or fresh weight, was always more abundant in the green than in the white.

Acidity.—The most painstaking studies have been made by Grandsire ('26), who obtained a low value for the total free or titratable acid content of pale areas in variegated leaves as compared to the green. Comparing the ash from chlorotic and green leaves with respect to combined acids (organic acid salts), the conclusion is reached that although the former leaves are higher in regard to total ash content they are actually lower with respect to combined acidity.

For the same samples this author found the ash of white leaves richer in soluble bases from the beginning to the end of the period of growth; the proportion of these bases increasing in albino leaves and diminishing in green leaves as growth continued. No electrometric titrations for total acidity or determinations for free hydrogen ions were made.

Presentation of Data

In addition to the work which was carried on at the Missouri Botanical Garden, a series of experiments was arranged at the Boyce Thompson Institute for Plant Research, at Yonkers, New York. It was hoped that they might lead to a better understanding of the nature of some of the effects which have been shown to occur when variegated foliage varieties have been placed under varying conditions of light and darkness and their leaf juices inoculated into healthy green varieties. Since some of the varieties used in the course of the experiments have been shown to be infectious variegations by Lindemuth, Baur, and others, interest in their behavior is stimulated by the fact that

after so many years so little is known in regard to the nature and cause of these diseases.

It has long been felt in the graduate laboratories at the Missouri Botanical Garden that this whole question should be reopened for further investigation with a view to relating the new and additional information to the general field of the mosaic and similarly classified diseases of plants. It was with such a purpose in mind that the following series of experiments was started. The first experiments to be described are physiological studies which have to do primarily with the influences of quality of light, intensity of light, and of darkness, all of which were considered by Baur in his researches upon infectious chlorosis.

THE EFFECT OF ENVIRONMENTAL FACTORS ON VARIEGATED LEAVES

EFFECT OF THE QUALITY OF LIGHT UPON THE PATTERN OF VARIEGATED LEAVES

Physical equipment.—The investigations were carried out in a range of five small adjacent greenhouses. These are referred to collectively as the spectral glass houses, inasmuch as they are equipped with sashes of different glasses especially selected for their ability to transmit certain wave lengths of the solar radiations and for holding back others. Each house was separately humidified and controlled with respect to temperature. The following table shows the glass used for each house and the wave lengths that it transmits.

TABLE II

WAVE LENGTHS INCLUDED IN THE VARIOUS VISIBLE AND ULTRA-VIOLET REGIONS AND SPECTRAL LIMITS OF GLASSES USED

Regions and glasses	Range in $\mu\mu$
Sunlight	290–720
Ultra-violet of sunlight	290–400
Violet	400–450
Blue	450–490
Green	490–535
Yellow	560–590
Orange	590–645
Red	645–720
Ordinary greenhouse glass (house I)	312–720
G 980 A. Corning (house II)	290–720
Noviol "O" Corning (house III)	389–720
Noviol "C" Corning (house IV)	472–720
G 34 (house V)	529–720

The relative intensity transmission was reduced in houses I

and II by means of shading inside with cotton netting so that these intensities would compare with those in the houses with limited spectra. On a very clear day the intensities in the different houses were measured with a Macbeth Illuminometer between 10:00 A.M. and 11:00 A.M., and they were each found to be approximately 3372 foot candles. Since the intensity of daylight varies from hour to hour and from day to day, no attempt was made to keep a constant record of it by measurements with a Macbeth Illuminometer or a pyroheliometer.

Plant material.—The varieties used in the first experiment were as follows: *Abutilon* var. *Savitzii; Evonymus japonica* L., varieties green, "*medio-picta,*" "*aureo-variegata,*" and "*argenteo-variegata;*" and *Pereskia aculeata* Mill., var. *Godseffiana,* and green. Both the green and the variegated varieties were placed in duplicate in each of the houses on September 24, 1926.

Results.—After two months under these conditions, the plants had produced an abundance of new growth. There seemed to be no observable correlations between the size, shape, or color of the light-pigmented leaf areas and the specific wave lengths transmitted in each of the houses. Except for an elongation of the internodes in the plants in houses IV and V, no striking changes could be observed in the general appearance of the plants nor of the foliage in one house as compared with another.

Material of *Abutilon Thompsonii* was available for use in late November, 1926, and ten plants were placed in each of the houses II, IV, and V, where they were left until the experiment ended on May 1, 1927. During the intervening months, variegated plants of the variety *Abutilon Thompsonii* under Corning glass G 980A in house II remained strongly variegated. The full intensity of the sunlight was permitted to enter the house.

Under the glass of both house IV (which excluded half of the blue rays) and house V (which excluded half of the green rays) all of the plants produced a very luxuriant growth. The variegated pattern of these plants changed noticeably from month to month during the winter and spring seasons. While most of the plants under normal greenhouse conditions retained the characteristic mosaic pattern without conspicuous modification, all of the plants in houses IV and V became less strongly varie-

gated. The yellow color in the chlorotic spots became less apparent in the older leaves, while in the newly developed leaves the spots were reduced in area as well as in the intensity of the yellow color.

To any one not already familiar with the extent to which the intensity and the duration of light may affect the variegation in leaves of *Abutilon Thompsonii,* it would appear reasonable to suppose that the quality of the light was the chief factor contributing to the condition of the chlorotic spots as described above. However, the author is disposed to consider the results as being brought about primarily by the shade which resulted from the nature of the glass used in houses IV and V. In all probability the short length of the winter days was a factor supplementing shade. It must be considered that each of these factors operated simultaneously in houses IV and V. In view of this fact, together with certain results obtained by the author showing the importance of the duration of the exposure to sunlight, the conclusion may be reached that a combination of the two factors, diminished intensity of sunlight and short day length, may account for the changed appearance of the variegated leaves.

EFFECTS OF CONTINUOUS ILLUMINATION

The experiments began on January 29 and officially ended, after a continuous run, on March 29. During this time the plants under the various conditions were examined daily, and extensive notes were taken describing their general appearance and especially the size and extent of the variegation developing in new leaves.

Physical Equipment.—The physical apparatus used in the control of the environmental factors for these experiments will be briefly described. The experiments were carried out under two sets of conditions, both available for use at the Boyce Thompson Institute. In one instance a gantry crane carrying forty-eight 1000-watt gas-filled lamps was used to supplement the sunlight of the day and was brought into action during the twelve hours of the night, being swung over the greenhouse shortly before sunset. The lamps were allowed to burn until shortly after sunrise. In the other instance a room humidified

and controlled with respect to temperature was lighted by means of twenty-five 1500-watt gas-filled lamps and three carbon arc lights suspended above a glass ceiling, which was kept flooded with water to eliminate direct heat rays. The lamps in this room burned steadily for twenty-four hours daily throughout the duration of the experiment. The plants were placed on a bench which circumscribed the room on three sides. The chief difference between the two conditions lies in the fact that plants were grown in the light room entirely under artificial illumination, while plants under the former condition received the daily sunlight and twelve hours of artificial light each twenty-four hours. The normal carbon-dioxide content of the air in both cases was supplemented by additional carbon dioxide from tanks under pressure. A self-recording electrical device was used to register variation in the concentration of the carbon dioxide in the vicinity of the plants under experiment, and meters were regulated to supply the gas uniformly. A house adjacent to the one receiving twenty-four hours of illumination accommodated all the control plants. This house was kept at a temperature of 78° F. with no extra light or additional carbon-dioxide gas. In a complementary experiment a small additional compartment under a roof of greenhouse glass was equipped with one 1000-watt electric lamp and a reflector. This was suspended above the tops of the plants at a height of two feet. All plants in this experiment received sunlight during the day and artificial illumination during the night.

Plant materials and methods.—Well-rooted cuttings of *Abutilon striatum* var. *Thompsonii* (pl. 6, fig. 1) and stout stock plants of the two *Evonymus japonica* varieties (pl. 6, fig. 3) showing new growth were placed under the conditions described above. Two entirely green plants of *Abutilon hybridum* with several green plants of *Evonymus japonica* were used as check plants under each treatment.

Representative plants from each condition were photographed on January 29 and were occasionally photographed thereafter until the end of the experiment two months later. Observations were frequently made. Samples were cut from chlorotic, green, and transitional areas of the leaves each week and then fixed in each of two killing fluids preparatory to embedding in paraffin.

Preliminary observations upon this cytological material will receive brief treatment under a separate heading. A presentation of cytological data in detail for the infectious variegations will appear soon in a subsequent paper.

Observations and conclusions.—The varieties of *Evonymus japonica* exhibited no visible or well-defined response to the conditions under which they were held while receiving continuous illumination, except for increases in stem growth. However, all plants of *Abutilon* showed an immediate response. All *Abutilon Thompsonii* held in the control greenhouse, 78° F., receiving no extra light and no extra carbon-dioxide gas, showed mottling only after the newly formed leaves reached a certain stage of development. Chlorotic areas never appeared before the new leaves were completely unrolled, but always before the leaves had been expanded for more than three to five days. The leaves at this stage enlarged exceedingly rapidly under all conditions and were capable of increasing in size from 16 sq. cm. to 64 sq. cm. in sixty hours. They may not have been visibly infected at the former size but they were in every case at the latter stage.

There seemed to appear first on these leaves very minute, lighter-colored islands, or flecks, which soon enlarged and coalesced with other flecks which were subsequently formed in the immediate neighborhood. An irregular, light-colored speck of a millimeter or so in diameter was produced by this fusion. It could be noticed that the first chlorotic flecks appeared frequently in the islands of parenchymatous leaf tissue which were in contact with the very finest tracheid endings. After a few days the leaves showed larger chlorotic areas, the size of fine bird shot, which were easily distinguished from the normal color. Later these yellow patches expanded to form still larger areas until they finally became limited by the larger vascular elements. From the course of the usual development, it can be said that the larger veins formed the boundary between the dark green and the lighter chlorotic areas. Typically mottled leaves of *Abutilon Thompsonii* under ordinary greenhouse conditions are shown in pl. 6, fig. 2. Just what factors in the leaves contribute to the production of such a uniformly mottled condition can not be explained at present.

Continuous 24-hour illumination.—Under the continuous 24-hour day in the light room, 78° F., with extra carbon-dioxide gas, with a battery of electric lamps and three carbon arcs to intensify the blue light, new leaves of *Abutilon Thompsonii* formed during the first ten days of the experiment became dark green, and so uniformly green, that unless they were examined under transmitted light they could not be distinguished from the leaves of normally green plants. A photograph showing these effects is given in pl. 7, fig. 1. In this paper the term "first-ranked leaf" will refer to the youngest expanded leaf at the growing tip; the "second-ranked leaf," to the next oldest leaf, etc. The upper and lower right-hand pairs of leaves in this photograph are taken from plants subjected to the same treatment and show the effect of the treatment on the variegation in different plants. In subsequent leaves the chlorosis developed as if its initial intensity had not been diminished.

As the experiment continued, mature leaves of the control green variety and all of the variegated plants of *Abutilon* became pale from an injury which may possibly be related to the quality of the light, its intensity, or perhaps to the absence of any period of rest. Chlorophyll was destroyed and in the case of the variegated *A. Thompsonii* the green areas disappeared temporarily, thereby leaving the leaves uniformly pale yellow in color. Photographs by transmitted light showed that the leaves possessed a mottling which had been masked by the acquisition of an additional chlorosis under the environment. New leaves of the variegated plants showed the infectious chlorosis as soon as plants in the control house, and in some cases sooner. The plants under continuous illumination were returned to the conditions in the control greenhouse at the completion of the experiments on March 29. Under these conditions new leaves developed free from the acquired chlorosis and mature leaves became plainly mottled.

Under the illumination of normal daylight together with the artificial light from a gantry crane, the condition of the plants under observation appeared to be essentially the same as that for the plants under continuous artificial light alone. *Abutilon Thompsonii,* however, did not show any decrease in the intensity

of the infectious chlorosis during the first ten days of the experiment, as was evident in the case of continuous artificial illumination.

EFFECT OF SHORT-DAY ILLUMINATION

Plants receiving light for five, seven or twelve hours in the continuous-light room were then shifted, according to the schedule, into a dark room where they were held at the same temperature and humidity without receiving light or extra carbon dioxide.

Five- and seven-hour day.—The conditions for growth appeared to be excellent for *Abutilon* but in the mature and new leaves the green areas developed somewhat less chlorophyll than the control plants. As the experiment continued, changes were apparent from week to week in the extent to which the chlorotic areas developed in newly formed leaves. Measurements were taken of the leaves when they first showed flecks, and these were compared with similar measurements taken in the control house and under the continuous-illumination experiments. The results suggest that although the first appearance of the infection may have been delayed to a certain extent, the chief difference lies in the rate at which the chlorotic areas enlarged, fused, and produced the mosaic pattern. As frequently observed under the five- and seven-hour-day length, the flecks first became visible by transmitted light when the leaves had an area of about 16 sq. cm. Upon developing an area of 61 sq. cm. it may be supposed, from the observations made upon the control and continuously illuminated plants, that the leaves should have a strong and well-defined mosaic pattern. However, this was not true in the latter case. For a few weeks after the new leaves reached this size under the shorter day lengths they still showed only traces of mottling. The axis of the main stem elongated much less rapidly under these short-day treatments than under the usual greenhouse conditions and the continuously illuminated environment.

On the other hand, where plants of Abutilon were grown under identically the same conditions except for twelve hours of artificial day and twelve hours of total darkness, the foliage remained brightly variegated, without change until near the end of

the experiments when some of the intensity of the chlorotic condition was lost. The fact that they then commenced to lose the variegation and to become more uniformly green may have been due to the slight fall in the intensity of the light in the continuous-light room, a condition which was observed during the last two weeks of the experiment.

Samples were taken and fixed for staining during the course of each week from one-half of the plants under each condition and from check plants held in the control greenhouse.

From time to time, free-hand sections were made of young leaves which developed under the above experimental conditions. The results will be given later in this paper.

On March 29, when the experiments ended, plants under the short-length days were photographed together with plants from all other conditions. All but two of the Abutilon plants under the five- and seven-hour length of day had a majority of uniformly dark green leaves as shown in pl. 9. A few old leaves in every case retained a somewhat faded mosaic pattern. These were already mottled before they were placed under the experimental conditions. In the case of the above exceptions, the plants were placed under the short-day treatment after the experiments were well under way, because they exhibited a very severe form of the chlorosis. While the intensity of the yellow color of the chlorotic areas became less in the younger leaves, these parts never approached the green condition as completely as did the others. In no instance did a plant become entirely free from all suggestion of the former variegated state. The faintest trace of a chlorotic condition could usually be observed in the younger foliage. After a time this became invisible so that the mature leaf was uniformly deep green. Minute isolated brown specks of dead tissue remained which did not occur in the green foliage of the control variety under the short days, so that in all probability we are correct in believing that these are due to the infectious chlorosis.

In the case of the varieties of *Evonymus japonica,* individual plants were equally liable to send out (1) a shoot entirely green, or (2) one entirely chlorotic. While the foliage in some plants of the var. "*aurea*" became more uniformly green under the

continuous illumination, there were plants in which the leaves became more deeply variegated. No generalizations could be drawn by attempting to attribute these characteristics to the influence of known environmental factors. In the short-day-length experiments the plants did not change their normal appearance.

Table III summarizes the plant material placed under each experimental condition.

SUMMARY OF THE RESULTS FROM DAY-LENGTH EXPERIMENTS

The chief observations from these studies under several degrees of illumination are as follows:

1. Under no conditions did the variegated varieties of *Evonymus* display the characteristics exhibited by *Abutilon striatum* var. *Thompsonii.*

2. While the young leaves of the control plants of *Abutilon striatum* var. *Thompsonii* became regularly infected, under continuous illumination they first became entirely green but those formed after the first two weeks became regularly and heavily infected.

3. New foliage appearing upon plants held under the five- and seven-hour-day lengths became entirely green in some cases and in other cases there was a strong tendency for the chlorotic areas to become fewer in number and reduced in size.

4. In no instance did the chlorotic areas of variegated leaves expand to embrace the entire leaf, that is, to cause the leaf to become uniformly yellow throughout.

THE EFFECT OF TOTAL DARKNESS

Four variegated plants each of *Abutilon Thompsonii, Evonymus japonica* varieties "*medio-picta*" and "*aurea*" were placed in the dark-room where the temperature and humidity were controlled as in the light experiments. Plants of *Abutilon* were the only ones to defoliate rapidly under these conditions. Two were taken into the light as soon as the stems were bared of leaves. The other two plants were kept in the dark for two weeks in which time they developed new top growth with etiolated leaves.

Each of the *Abutilon* plants taken in the light developed numerous small green leaves along the stem, and the greater

TABLE III

DAY-LENGTH EXPERIMENTS

Species and varieties	24 hrs. per day, continuous-light, + gas, temp. 78° F.	12 hrs. sunlight, 12 hrs. artif. light, gas, temp. 78° F.	19 hrs. dark, 5 hrs. light, temp. 78° F.	17 hrs. dark, 7 hrs. light, temp. 78° F.	12 hrs. dark, 12 hrs. light, temp. 78° F.	Control 78° F.
Abutilon striatum						
var. "*Thompsonii*"	6 plants	14 plants	4 plants	4 plants	4 plants	14 plants
Abutilon hybridum (green)	3 plants	2 plants	1 plant	1 plant	1 plant	2 plants
Evonymus japonica						
var. "*aureo-variegata*"	5 plants	10 plants	2 plants	2 plants	2 plants	13 plants
var. "*medio-picta*"	5 plants	10 plants	2 plants	2 plants	2 plants	13 plants
var. green	2 plants	5 plants	1 plant	1 plant	1 plant	5 plants
Total number of plants under each experiment	21	41	10	10	10	47

number of these later became severely chlorotic and remained dwarfed and sickly. The two plants which were kept in the dark-room for a longer time were eventually taken into the continuous-light room where it was noticed that the etiolated leaves became uniformly green and remained so. However, new leaves that were allowed to develop at the growing tip of the stem in the light became variegated and remained so, but the originally etiolated leaves which later developed chlorophyll never became visibly reinfected. From the experience of the author the effects which Baur attributes to the influence of complete darkness may have been due primarily to the loss of variegated foliage, a factor which will be considered in a later experiment.

Histological Studies

HISTOLOGICAL STUDIES OF ABUTILON THOMPSONII SUBJECTED TO VARIOUS CONDITIONS OF LIGHT

It is well known, histologically, that variegations may be of two types, those in which the green and the chlorotic areas are arranged in sharply differentiated sectors and layers such as the so-called chimeras; or those in which the chlorotic and the green areas are not sharply defined, the affected cells exhibiting chloroplasts in all stages of dissolution from normal plastids to complete disintegration of the contents.

In the present discussion we are chiefly interested in the latter group to which *Abutilon Thompsonii* and other infectious chloroses belong. In the leaves of this plant there was a gradual transition from the normal green tissue to chlorotic, as free-hand sections of living leaf tissue showed. No particular hyperplasia or hypoplasia could be noticed in sections through chlorotic and normal areas. Although intensely variegated material was studied under ordinary magnifications of a high-power dry objective, no consistent differences in structure could be observed between the green and the chlorotic areas, thus confirming the earlier observations of Zimmerman ('92) and Baur ('08).

Method.—Cytological material was obtained from the plants from all previously described experiments, including the control plants, which can be collectively referred to as light treatments, except the experiments which were carried out in the spectral

houses. Care was taken that the sampling should be comparable in so far as the age and the chlorotic appearance of the leaf were concerned. As an additional precaution the length, width, and the rank of each leaf sampled was recorded for each plant, together with a simple description of its variegated appearance.

The fixing agents were made up as follows:

1. Formalin (40 per cent) . . . . 5 cc.
   Alcohol (75 per cent by vol.) . . . . 100 cc.
   Glacial acetic acid . . . . 5 cc.
2. Corrosive sublimate, saturated in 50 per cent alcohol.

In the former fluid, the tissues may be stored indefinitely or until they can be conveniently dehydrated and imbedded in paraffin. The latter fixing agent was used while hot. The excess mercuric chloride was precipitated with iodine solution in the process of dehydration to 80 per cent alcohol.

Only a small proportion of the total material collected throughout the course of the light treatments has been sectioned and stained to date. The present data represent a portion of the material of *A. Thompsonii* which was collected between February 1 and 16, which included exactly one-fourth of the duration of the light treatments. The slides were stained with Haidenhain's iron-alum haematoxylin and counterstained with orange G. They were studied with a Leitz microscope equipped with a 1/10a fluorite or semi-apochromatic objective, with a numerical aperture = 1.30. All the drawings given in pl. 5 were made with the aid of a Spencer camera lucida and are of equivalent magnifications. It is intended that the drawings be considered semi-diagrammatic.

Observations.—Striking modifications were found in the leaf tissue of plants which were subjected to the light from the gantry crane in addition to daylight. Figure 2 of pl. 5 shows that the leaf at the beginning of the experiment was nearly normal except for the presence of unusually large intercellular spaces even in the palisade layer. Figure 1 of pl. 5 shows the condition in a leaf of an age comparable to that in pl. 5, fig. 2, after the experiment had been running for two weeks. The outstand-

ing modifications in the anatomical structure as a result of the continuous light are: increase in size of cells, increase in number and size of intercellular spaces, both of which contribute to the increase in thickness of the leaf. In addition, the cells have become literally packed with chloroplasts, so that it may be concluded that continuous light brings about an increase in number of chloroplasts as well as in thickness of leaves.

As opposed to the modifications in leaf anatomy which were brought about by continuous lighting in which daylight is supplemented by the gantry crane, are those resulting from subjecting the plants to the short or five-hour day. Figure 5 in pl. 5 shows the condition at the beginning of the experiment, and, as would be expected, is quite similar to fig. 2, pl. 5, both of them representing leaf structure after the experiment had been under way but a few days. Figures 6 and 7 represent the situation two weeks later and present modifications exactly the opposite to those found in leaves of plants which were kept under continuous illumination. The cells are a great deal smaller, and the intercellular spaces have become essentially negligible even in so short a time. The palisade layer is scarcely discernible. Chloroplasts appear to be smaller and fewer in number than in the cells at the beginning of the experiment. It was difficult in fixed material to distinguish between chlorotic and green areas.

In no case were cellular inclusions of the nature of the X-bodies of tobacco and other members of the Solanaceae infected with true mosaic disease observed in the Abutilon material which has been studied.

EXPERIMENTS ON THE INFECTIOUS PROPERTIES OF VARIEGATIONS

INOCULATION EXPERIMENTS

To date, one of the fundamental distinctions between the "infectious chlorosis" of *Abutilon* and the mosaic disease of tobacco lies in the fact that the former has been transmitted only by grafting whereas with the latter infection results readily from inoculation with the juices of the diseased plants. Consequently, all the possibilities for bringing about infection by inoculation should be tried, since the results may lead to a closer understanding of the principles underlying some of the facts

which are being discovered in connection with the virus diseases of plants. There are things to be said in favor of a new type of inoculation experiment in which the atmospheric environment of the virus and the oxidation processes of the expressed juices are made to simulate the conditions in the living cell.

Elmer ('25) has reported successful transmissions of sugar-cane virus to tobacco and of other mosaics which have proved difficult to cross-inoculate, by using an inoculum mixed with a 30 per cent solution of acetone. Vinson ('27) claims that the virus of tobacco can be concentrated by acetone and regained from solution by precipitation and inoculated without loss of infectiousness. The plant materials which he used were frozen before the juice was expressed.

Materials and method.—Leaves of *Evonymus japonica* vars. "*aurea*" and "*medio-picta*" were treated in the following way. The yellow areas were cut out and considered separately from the green areas. Both the green and the yellow portions were frozen for forty-eight hours before the juices were expressed. In order to obtain the juice the leaf materials were ground in separate mortars to which were added 2 cc. of a 30 per cent solution by volume of one of the following: acetone, ethyl alcohol, glycerine, and toluene. The resulting mixture was inoculated immediately. Samples of juice were also obtained from leaves which were not ground up with reagents. The plants to be inoculated were trimmed of all shoots and branches except two main stems, in order to stimulate new growth. The tip of one branch was cut off preliminary to an inoculation with a hypodermic needle into the pith of the stem. Inoculations were made on September 18, 1926.

Sixteen plants were grouped into four lots of four each. Half of the plants in each lot received expressed juice plus one of the above-mentioned reagents, while the other half received unadulterated juice. Two samples of juice expressed from yellow areas, that is, one with and one without the addition of an organic solvent, were inoculated into various parts of the stem and leaves by the following methods. On each plant some of the leaves were scratched with a needle and the inoculum applied from a pipette. Old leaves and very young leaves were treated alike.

Stabs with the point of a scalpel were made along the stem in three places, beside the axillary buds near the base of the stem, midway, and near the growing apex. Inoculations of the juice were made in two of these wounds, and a paste of leaf pulp (the residue after maceration) was placed in a third wound and bound with tape. A hypodermic syringe was used to inject the inoculum under pressure into the pith of the stem, the succulent parts of the stem, and the petioles of leaves. The entire experiment was repeated, using green areas instead of the chlorotic, thereby making a total of thirty-two plants in the experiments.

Results.—There were no positive indications of the transmission of the chlorosis in any of these plants during the subsequent year and a half. Experiments in which the juice from crushed leaves of *Abutilon striatum Thompsonii* have been inoculated into green plants of *Abutilon* have not resulted in the transmission of the variegation.

GRAFTING AND BUDDING EXPERIMENTS

Grafting and budding experiments were carried on in March, 1927, with the same varieties of *Evonymus* that were used in the inoculation experiments. In most cases the grafted scions of the variegated and the green plants died after a period of two weeks. From a total of fourteen grafts four lived.

In the case of two of the grafted plants of the variety "*aurea*" which survived, there was a definite transmission of the infectious chlorosis from a variegated scion to a green stock six weeks from the date that the graft was made. The chlorosis began to appear on one of the first leaves to mature, and at first it could be distinguished on close examination by a clearing of the larger veins. After two more weeks had elapsed, the chlorosis had traversed to all of the smaller vascular elements which lead to the interstices between the veins. By strong transmitted light it appeared as an indefinite mottling in the interstices. It was expressed uniformly throughout the entire leaf and was differentiated into very indistinct chlorotic and green areas, the outlines of which could scarcely be distinguished because of their minute size. Neither Bouché ('71), Baur ('08), nor Rischkow ('27b) have included in their papers photographs of the chlorosis

with which they were dealing, but from their descriptions it would seem that the chlorosis just described is identical with theirs. A photograph taken by reflected light of detached leaves exhibiting this peculiar type of infectious chlorosis, also a variegated leaf of the variety "*aurea*" from which the infectious chlorosis was obtained by grafting, is shown in pl. 11. Plate 11, fig. 2, also includes a photograph of a detached leaf from the non-infectious variety, "*medio-picta.*"

Of the four successful grafts which survived, two others, one of "*medio-picta*" on a green stock and one of green on a stock of the variety "*aurea,*" did not show any transmission of the chlorosis during the following eighteen months.

In addition to the successful transmission of the infectious chlorosis by grafting, it has been possible to transmit the chlorosis also by budding. Dormant buds of the variety "*aurea*" were inserted into the bark of ten normal green plants of *Evonymus.* A fairly high percentage of the buds lived for more than one month but eventually died. Two months after the death of the buds, on one of the plants the typical symptoms of this infectious chlorosis began to appear on the younger mature leaves.

Although the author has been unable thus far to graft variegated varieties of *Abutilon* with the green, there is no reason to believe that such transmissions of the chlorosis for the variety "*Thompsonii*" should prove impossible. Plate 7, figs. 2 and 3 are taken from figures of Lindemuth ('99a) and ('07) respectively, and show definitely that he was able to transmit the chlorosis of *Abutilon Thompsonii* to other members of the Malvaceae. Plate 8, fig. 1, is a photograph of infectious chlorosis on *A. megapotamicum,* which is included in order to show an infectious chlorosis on another species of *Abutilon.*

EFFECT OF THE REMOVAL OF VARIEGATED LEAVES

It has been reported by Baur that *Abutilon* infected with chlorosis can be made to lose all evidence of the disease by stripping off repeatedly all the leaves from the stem. Then by removing the leaves which show infection from each new crop for several successive crops, the leaves of the plant will eventually

develop and remain normal green without further evidence of previous infection. This is an experiment which he accomplished in the light.

It has been the writer's experience that this "curing" process can be accomplished but that it is accomplished gradually over quite a period of time. In the greenhouses at the Boyce Thompson Institute, Doctor L. O. Kunkel has had strongly variegated plants of *Abutilon Thompsonii* under his observation for three years. With one of them he followed the procedure which Baur used and removed the variegated leaves. The leaves on the other plant were allowed to remain on the stem. The photograph in pl. 11, fig. 1 was taken by the writer April, 1927, and shows the condition of the plant after three years. According to Baur, the "cured" plant on the right in the picture would be susceptible to subsequent infection if grafted with *Abutilon Thompsonii*, an experiment which has not as yet been carried out by Doctor Kunkel. The obvious experiment of grafting the "cured" stem back upon a green susceptible stock of *Abutilon* has not been tried, although it is acknowledged that such an experiment is necessary before it can be established conclusively whether or not a variegated individual can be "cured" and retain and transmit the infectious agency.

Biochemical Studies

VARIEGATED LEAF PIGMENTS

The author held the view that quantitative determinations of variegated leaves might present data which would indicate the presence of chemical disturbances affecting the normal molecular ratios of chlorophyll a/chlorophyll b and carotin/xanthophyll. Thus, certain indications might be gained as to the probable sequences in the development of chlorosis.

Quantitative determinations of chlorophyll and carotinoid pigments have been made on the leaves of *Abutilon Thompsonii* and a green variety of *Abutilon*. The chlorophyll fractions were determined as phytochlorin-E and phytorhodin-G which were made up to volume with appropriate concentrations of hydrochloric acid and compared colorimetrically with Guthrie's standards (see Guthrie, '28). The data are withheld, however, until the results from further analyses will justify conclusions.

ACIDITY DETERMINATIONS

ELECTROMETRIC DETERMINATIONS OF HYDROGEN-ION CONCENTRATION

Apparatus.—By including the recently developed quinhydrone electrode system with the calomel cell which Hildebrand ('13) used with the normal hydrogen electrode, a remarkably inexpensive instrument, easy to operate, can be made for the determination of hydrogen ions. Such an apparatus was built by the author following the suggestions made by Dr. William Youden,[1] at the Boyce Thompson Institute.

Since in these experiments it was necessary to use a fraction of one cc. of the leaf juices for a single reading, and since for an ordinary platinum electrode there is needed at least 2 cc. of a solution, the method was modified to determine the acidity in a single drop of the sample. To do this a thin strip of copper foil about 2 cm. wide was used in the circuit. This served to support the platinum electrode which consisted of a flat plate of platinum foil carefully depressed on one surface to hold about one or two drops of the sample liquid. Contact between the platinum and the copper strip was assured by depressing the surface of the latter to correspond exactly with that of the platinum both as to shape of the indentation and as to its depth. Contact between the calomel electrode and the sample drop was made in the usual way by means of an agar salt bridge of saturated potassium chloride solution. However, care was taken to avoid a siphon action in all cases where the solution of potassium salt was used, by plugging the open end which extended into the calomel cell with cotton and by drawing the opposite end to a capillary point.

Method.—The hydrogen-ion concentrations of leaf juices expressed from the green and lighter pigmented areas of variegated leaves have been determined electrometrically by the quinhydrone method for all varieties of *Evonymus japonica,* representative leaves of which are shown in pl. 8, fig. 2. In all cases the initial acidity of the juice was determined quickly and recorded. In

[1] Dr. Youden perfected the "Youden Hydrogen Ion Outfit," which is being sold by the W. M. Welch Scientific Company of Chicago. For a complete description of the apparatus, including directions for the use of materials, the electrical instruments, and the mechanical features incident to the electrical wiring, the reader is referred to these authorities.

the case of certain samples the juice was permitted to stand in air and subsequent determinations were made from it at stated intervals of time varying from a few to several minutes.

The procedure was as follows: Leaves were taken from a particular variety of *Evonymus*, and in determinations where variegated leaves were used the dark and light areas were carefully cut out. These portions of the leaves were ground separately in individual mortars. The determinations were carried out at once upon the undiluted juices which were expressed by the grinding operation. Quinhydrone crystals, in a quantity sufficient to be easily carried on the pointed tip of a scalpel blade, were added to each sample before the determination was made. This mixture was quickly brought to a condition of equilibrium by stirring with the tip of a very fine glass rod. The capillary point of the salt bridge was placed in the drop of sample and a reading was taken immediately.

The difference in potential between the saturated calomel electrode standard and the quinhydrone electrode at the equilibrium of the system was observed as voltage on a Weston millivoltmeter. The pH of the sample was read directly from a table constructed from a formula relating the voltage of a calomel-quinhydrone system to pH, at a temperature of 25° C. When the room temperature ranged above this value the readings were corrected accordingly. The formula for the conversion of the quinhydrone electrode E.M.F. to pH, when a saturated calomel reference electrode = 0.2464 volts at 25° C. was used, is as follows:

$$\text{Formula:}\quad pH = \frac{.699 - E - .246}{.0591}$$

When solutions are more acid than pH = 7.66, the calomel is negative and the quinhydrone electrode is positive. Using solutions more alkaline than pH = 7.66, the calomel is positive and E has a negative value in the formula. The lead wires, *g* and *h* in pl. 10, connecting the voltmeter, *m*, and the galvanometer, *n*, with the calomel cell and the quinhydrone electrode respectively, depend for their respective positions upon the degree of acidity of the solution in question. When solutions are more acid than pH = 7.66, the calomel is connected with the circuit by

TABLE IV

COMPARISON OF INITIAL ACIDITY IN CHLOROTIC AND GREEN TISSUES

Variety used	No. of plants in sample	Green		Chlorotic	
		$(H+)^{10^{-6}}$	pH	$(H+)^{10^{-6}}$	pH
	7	.363	6.44	.85	6.07
	7	.257	6.59	.85	6.07
	7	.295	6.53	—	—
	7	.388	6.41	.955	6.02
"*medio-picta*"	1	.257	6.59	.456	6.34
	1**	.218	6.66	.575	6.24
	1**	.308	6.51	.757	6.12
	1*	.456	6.34	.708	6.15
	1	.257	6.59	.240	6.62
	19	.295	6.53	.575	6.24
	5	.426	6.37	.363	6.44
	5	.388	6.41	.436	6.36
	1*	.234	6.63	.104	6.98
	1*	.456	6.34	.308	6.51
	1**	.218	6.66	.263	6.58
	1**	—	—	.288	6.54
	1*	.562	6.25	.794	6.10
"*aurea*"	1*	.562	6.25	.562	6.25
	1**	.380	6.42	1.26	5.90
	1**	.436	6.36	1.35	5.87
	10	.380	6.42	.209	6.68
	4	.295	6.53	.380	6.42
	5	.295	6.53	.257	6.59
	1	.338	6.47	—	—
	5	.456	6.34	.436	6.36
	4	.812	6.09	1.41	5.85
	4	.536	6.27	1.32	5.88
	1	.812	6.09	.955	6.02
"*argenteo*"	4	.562	6.25	—	—
	1	.812	6.09	1.26	5.90
	1	.812	6.09	1.32	5.88
	1	1.00	6.00	2.22	5.65
	1	.562	6.25	1.78	5.75
	1	.209	6.68	—	—
	1	.245	6.61	—	—
	1*	.186	6.73	—	—
	1**	.675	6.17	—	—
	1*	.257	6.59	—	—
	1*	.257	6.59	—	—
green	1*	.288	6.54	—	—
	1*	.308	6.51	—	—
	1	.812	6.09	—	—
	1*	.234	6.63	—	—
	1*	.209	6.68	—	—
	31	.675	6.17	—	—
	31	.725	6.14	—	—

* = young and very young leaves; ** = old and very old leaves.

means of lead wire, *g*, and the quinhydrone-platinum electrode is

connected by means of *h*. They are interchanged for solutions more alkaline than pH = 7.66.

Tests were made repeatedly throughout the course of the experiments, using buffer solutions of known pH to ascertain the degree of accuracy of the single-drop method, as opposed to electrometric methods where larger samples of the buffers were used. The instrument was found correct within 0.03 pH.

Full directions for the preparation of calomel electrodes are given by Findlay ('20, pp. 228–230), and by Clark ('20, pp. 133–134). Many suggestions are made by these authorities which are of assistance in measuring acidity with the quinhydrone electrode system. It should be borne in mind that, because of its simplicity and the convenience with which it can be used in the field, a M/20 potassium acid-phthalate solution makes probably the most satisfactory reference electrode that the biologist can use.

Results.—The data from the hydrogen-ion determinations are given in tables IV, V, VI, and VII. The results which are included in these tables are a fair representation of the results from nearly 400 determinations, many of which are not given in this paper for lack of space.

TABLE V

COMPARISON OF YOUNG AND OLD LEAVES AS TO INITIAL ACIDITY

Variety used	No. of plants in sample	Young leaves				Old leaves			
		Green		Chlorotic		Green		Chlorotic	
		$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH
"*medio-picta*"	1	.257	6.59	.456	6.34	.218	6.66	.575	6.24
	1	.456	6.34	.562	6.25	.308	6.51	—	—
"*aurea*"	1	.234	6.63	.166	6.78	.245	6.61	.263	6.58
	1	.456	6.34	.308	6.51	—	—	.288	6.54
	1	.562	6.25	.794	6.10	.380	6.42	1.26	5.90
	1	—	—	—	—	.436	6.36	1.35	5.87
"*argenteo*"	1	.812	6.09	1.32	5.88	1.00	6.00	1.78	5.75
	1	—	—	—	—	.562	5.25	1.78	5.75
	1	—	—	—	—	—	—	2.22	5.65
green	1	.186	6.73	—	—	.675	6.17	—	—
	1	.256	6.59	—	—	—	—	—	—
	1	.256	6.59	—	—	—	—	—	—
	1	.288	6.54	—	—	.308	6.51	—	—
	1	.234	6.63	—	—	.209	6.68	—	—

CHLOROTIC AND GREEN AREAS

A comparison of the initial acidities for the green and the chlorotic areas of all the variegated varieties of *Evonymus* included in the present paper indicates that the chlorotic areas are higher in initial acidity than the green for all varieties except "*aurea.*" Arranged in the order of descending values, they are "*argenteo,*" "*medio-picta,*" and "*aurea.*" The data suggest that in the white variegated variety, "*argenteo,*" the chlorotic areas have a consistently higher initial acidity than the chlorotic areas of any other variety.

YOUNG AND OLD LEAVES

While the chlorotic areas were found to have a higher initial acidity in old leaves than in young leaves, the green areas were more acid. Old leaves of the normal green variety were higher in (H^+) concentration than the young leaves.

EFFECT OF FREEZING

Freezing the leaves just prior to expressing the juice increased the acidity of the juice of both the green and the chlorotic areas. For data in addition to that given in table VI reference should

TABLE VI

EFFECT OF FREEZING ON INITIAL ACIDITY

Variety used	No. of plants in sample	Frozen				Non-frozen			
		Green		Chlorotic		Green		Chlorotic	
		$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH	$(H+)^{10-6}$	pH
"*medio-picta*"	1	.275	6.56	.812	6.09	.257	6.59	.575	6.24
	1	.308	6.51	.812	6.09	.256	6.59	.600	6.22
green	1	.346	6.46	—	—	.209	6.68	—	—

be made to text-figs. 2 and 3, in which the initial acidity determinations in the titration experiments on juices from frozen and fresh tissues exhibited the same phenomenon.

EFFECT OF EXPOSURE TO AIR

As mentioned in the discussion of the method, several determinations were made at stated intervals of time upon samples of

juice which were being exposed to air. It was observed that for all samples of juice there was a decided increase in the acidity which was roughly proportional to time, as is indicated by the

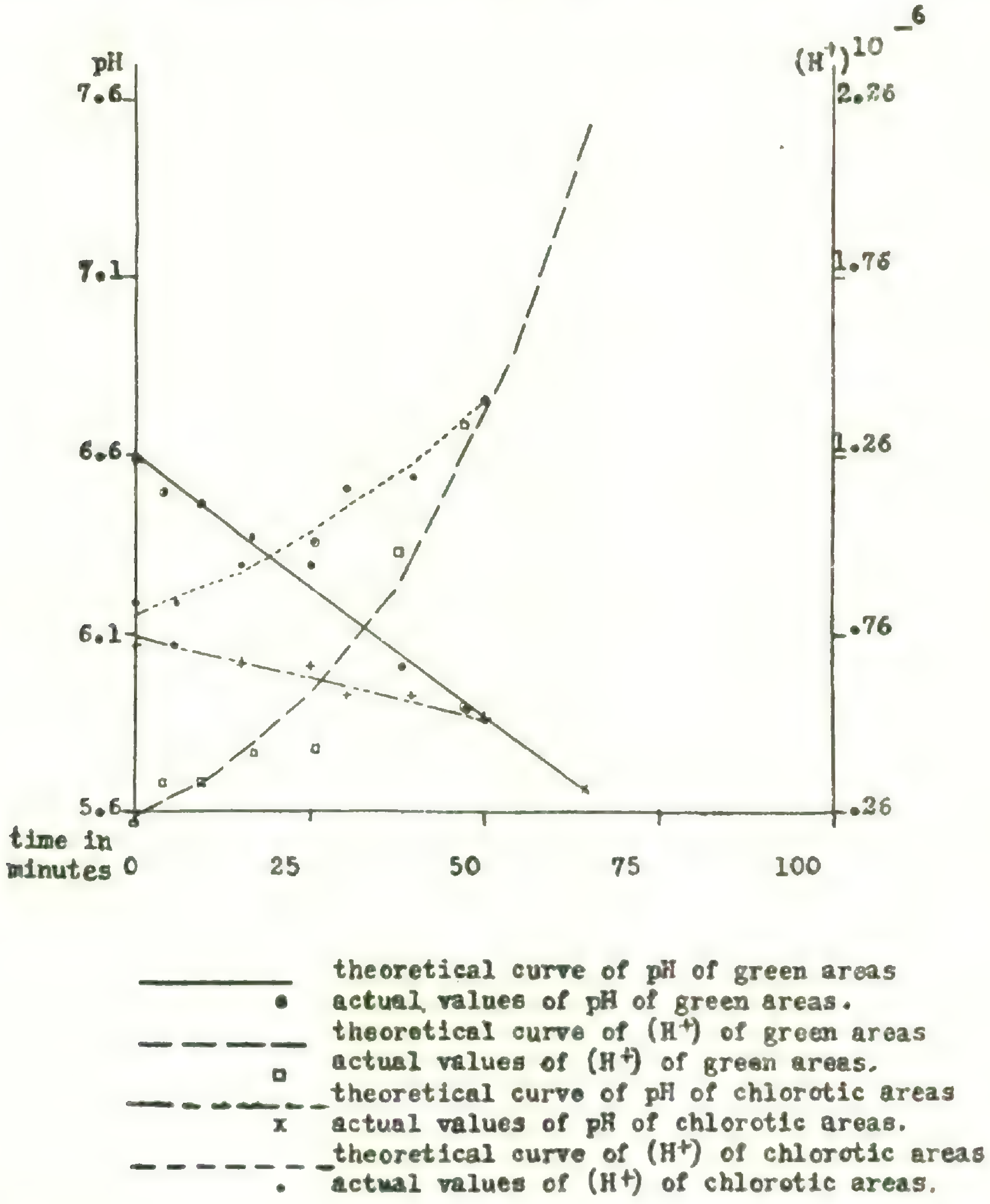


Fig. 1 Progressive changes in pH and (H^+) with time of exposure of juice to air.

data furnished in table vii and text-fig. 1. It will be noticed at once from the points on the graph that the pH of the juice from green and chlorotic samples decreased steadily throughout

the course of the experiment; that is to say that the acidity of the juice increased steadily. The points on the graph, where pH is plotted against time for both green and chlorotic leaf areas

TABLE VII

EFFECT OF EXPOSURE TO AIR ON THE ACIDITY OF EXPRESSED JUICE

Variety used	No. of plants in sample	Green			Chlorotic		
		Time min.	$(H+)^{10-6}$	pH	Time min.	$(H+)^{10-6}$	pH
"*medio-picta*"*	7	0	.257	6.59	0	.85	6.07
		4	.324	6.49	6	.85	6.07
		9	.338	6.47	15	.955	6.02
		17	.426	6.37	25	.955	6.02
		26	.436	6.36	30	1.17	5.93
		38	1.00	6.00	39	1.20	5.92
		47	1.35	5.87	50	1.41	5.85
"*aurea*"	5	0	.426	6.37	0	.218	6.66
		4	.675	6.17	6	.257	6.59
		9	.708	6.15	12	.295	6.53
		15	.795	6.10	21	.308	6.51
		23	.955	6.02	26	.436	6.38?
		28	1.00	6.00	32	.537	6.27
		36	1.07	5.97	36	.575	6.24
		46	1.20	5.92	47	.812	6.09
		96	1.74	5.76	62	.955	6.02
"*argenteo*"	4	0	.537	6.27	0	1.32	5.88
		3	1.26	5.90	6	1.32	5.83
		5	1.26	5.90	10	1.55	5.81
		8	1.48	5.83	15	1.58	5.80
		14	1.62	5.79	21	2.18	5.66?
		18	2.09	5.68	24	1.74	5.76
		24	2.63	5.58	29	1.95	5.71
		28	2.95	5.53	37	1.99	5.70
		34	2.88	5.54	55	2.18	5.66
		37	3.08	5.51	65	2.45	5.61
		41	3.08	5.51	—	—	—
green	1	0	.209	6.68			
		2	.199	6.70			
		5	.209	6.68			
		9	.257	6.59			
		15	.288	6.54			
		19	.380	6.42			
		23	.388	6.41			
		27	.513	6.29			
		41	1.00	6.00			

* Data show agreement with theoretical linear curves to within an average deviation of 0.03. See text-fig. 1.

of the variegated variety "*medio-picta,*" show a close agreement with a linear function when they are fitted in the equations

$$(1) \quad m = \frac{n\Sigma(xy) - \Sigma xy}{n\Sigma(x^2) - (\Sigma(x))^2}$$

$$(2) \quad b = \frac{\Sigma y - m\Sigma(x)}{n}$$

and when these values are further substituted in the equation

$$(3) \quad y = mx + b$$

y = actual pH
x = time interval
m = factor for equation (1)
b = value for equation (2)

The deviation of each point from the straight-line curve is expressed as the difference between the actual pH values determined in the experiment and the theoretical values for pH as calculated from the above equations. These numerical values are shown in table VIII. In text-fig. 1, the average deviation of all points from the theoretical curve is less than 0.03 pH, which is in agreement with the limits of the experimental accuracy for this type of potentiometer and with the method used in making the determinations.

ELECTROMETRIC DETERMINATIONS OF TOTAL ACIDITIES

Apparatus.—In addition to the electrical instruments used in the determinations of hydrogen-ion concentrations by the quinhydrone electrode method, the apparatus was modified to include the following additional equipment, as shown in pl. 10.

A platinum electrode was made by sealing a triangular piece of platinum foil, measuring from 1.5 to 2.0 cm. from base to apex, into the molten end of a glass tube, *a*, having a bore of approximately 3 mm. The tube was partially filled with mercury to insure a suitable contact between the platinum foil and an insulated copper lead wire about number 26 D.S.C. The necessity for rigging a separate stirring device was alleviated by rotating the glass tube, *a*, in the vial, *b*, which also contained the quinhydrone-platinum electrode system, one end of the salt bridge, *c*, the tip of the burette, *d*, and the plant juice which was to be titrated. The saturated calomel cell, *e*, was indirectly

TABLE VIII

ACTUAL AND THEORETICAL VALUES FOR PH AND (H^+) FOR DATA PLOTTED IN TEXT FIG. 1

Tissue	pH				(H^+)$^{10^{-6}}$			
	Time min.	Theoretical value	Actual value	Difference	Time min.	Theoretical value	Actual value	Difference
Green	0	6.60	6.59	.01	0	.251	.257	.006
	4	6.54	6.49	.05	4	.288	.324	.036
	9	6.47	6.47	.00	9	.339	.339	.000
	17	6.35	6.37	.02	17	.447	.426	.021
	26	6.22	6.36	.14	26	.603	.436	.167
	38	6.04	6.00	.04	38	.912	1.00	.088
	47	5.89	5.87	.02	47	1.29	1.35	.06
	54	5.81	—	—	54	1.55	—	—
	59	5.73	—	—	59	1.86	—	—
	64	5.66	—	—	64	2.19	—	—
Chlorotic	0	6.09	6.07	.02	0	.812	.85	.038
	6	6.06	6.07	.01	6	.87	.85	.02
	15	6.03	6.02	.01	15	.932	.955	.023
	25	5.98	6.02	.04	25	1.04	.955	.085
	30	5.95	5.93	.02	30	1.12	1.17	.05
	39	5.91	5.92	.01	39	1.23	1.20	.03
	50	5.80	5.85	.01	50	1.41	1.41	.000

connected with the vial, *b*, by means of the salt bridge, one end of which dipped into a saturated KCl solution in vial, *f*. This solution was also in contact with the tip of the side-arm of the calomel cell. When in use, the salt bridge must be filled with a saturated solution of KCl, the end in vial, *f*, may be plugged with cotton, and the opposite end in vial, *b*, may be drawn to a capillary fineness to prevent a siphon action between the vials.

Lead wires, *g* and *h*, connecting the voltmeter, *m*, and galvanometer, *n*, with the calomel cell and the quinhydrone electrode respectively, must be interchanged during the course of the titration according to the degree of acidity of the solution under examination. For the procedure with solutions more alkaline than pH 7.66, directions have been given in the discussion of electrometric determinations of hydrogen-ion concentrations. Reference has also been made to the sources of information concerning the use of materials and electrical instruments, as well as to the mechanical features incident to the electrical wiring.

Power for turning the stirring apparatus was furnished by means of a small electric motor, *i*, to which the pulley and cords were arranged as shown in pl. 10. Using the glass tube of the platinum electrode as a stirring rod and the exposed blade of the platinum foil as a paddle necessitated an arrangement providing for the rotation of the shaft, which must be held in place and rigidly supported in order to insure a true circular motion. The shaft was made to fit snugly into the bore of a short piece of glass tubing, *k*, which shall be referred to as a sleeve. The sleeve, although carefully selected to avoid undue friction and too much play, was lubricated with vaseline, and when in operation served as a well-lubricated bearing. The sleeve was fitted tightly into a one-hole rubber stopper which was clamped securely to an iron stand. In a similar way, the shaft was fitted into a one-hole rubber stopper which plugged a hole centrally located in a pulley rotating in a plane perpendicular to the shaft. A metal washer, *l*, was inserted between the rubber stoppers to increase efficiency.

For the titration of 1- to 2-cc. quantities of plant juice, it was necessary to use a burette of very small dimensions. A satis-

factory burette[1] can be made from a straight pipette having a capacity of 2 cc. and graduated in hundredths cc.

Materials and methods.—The plant materials used were the leaves of *Evonymus japonica*, variety green and variegated varieties "*aurea*" and "*medio-picta.*" The juice was expressed by means of a hydraulic press at a pressure approximately equal to 10–15 pounds per square inch. The juice was always filtered quickly through cheese-cloth and titrated at once or allowed to stand, depending upon the conditions of the experiment. In some instances the leaves were frozen at a temperature of $-19°$ C. in a cold room before pressure was applied. In other experiments the leaves were permitted to stand for an equal period in a room where the temperature was cool, but never fell below 5° C. The experiments were carried on during the month of August in Yonkers, N. Y. The leaves were stripped from plants which had been growing in an outside garden for three months.

Twentieth normal and fiftieth normal NaOH and HCl solutions were made up from reagents of C.P. quality and stored in Jena flasks with ground-glass stoppers, for the duration of the experiments. Titration curves of N/20 and N/50 NaOH with HCl are included with the data from the titration of NaOH against the plant juice extracts.

EFFECT OF FREEZING ON BUFFER ACTION

Method.—Variegated leaves of *Evonymus japonica* var. "*aurea*" were collected at 6:00 P.M. and were then divided into two lots. The leaves of one lot were kept entire. The second lot was subdivided, the yellow areas being cut out from the green and considered separately. Each of the three lots of tissue (entire leaves, yellow areas, and green areas) were divided equally, one-half being left to freeze over night, the other half kept above freezing for the same interval of time. During the course of the following day, juice was expressed from each fraction and titrated immediately with N/50 NaOH. Duplicate titrations were made on each sample and the resulting curves showed remarkably

[1] The burettes, *d*, which are shown in pl. 10, were made up for the author by Eimer & Amend Company in New York.

close agreement. The results from the titrations are shown in text-fig. 2.

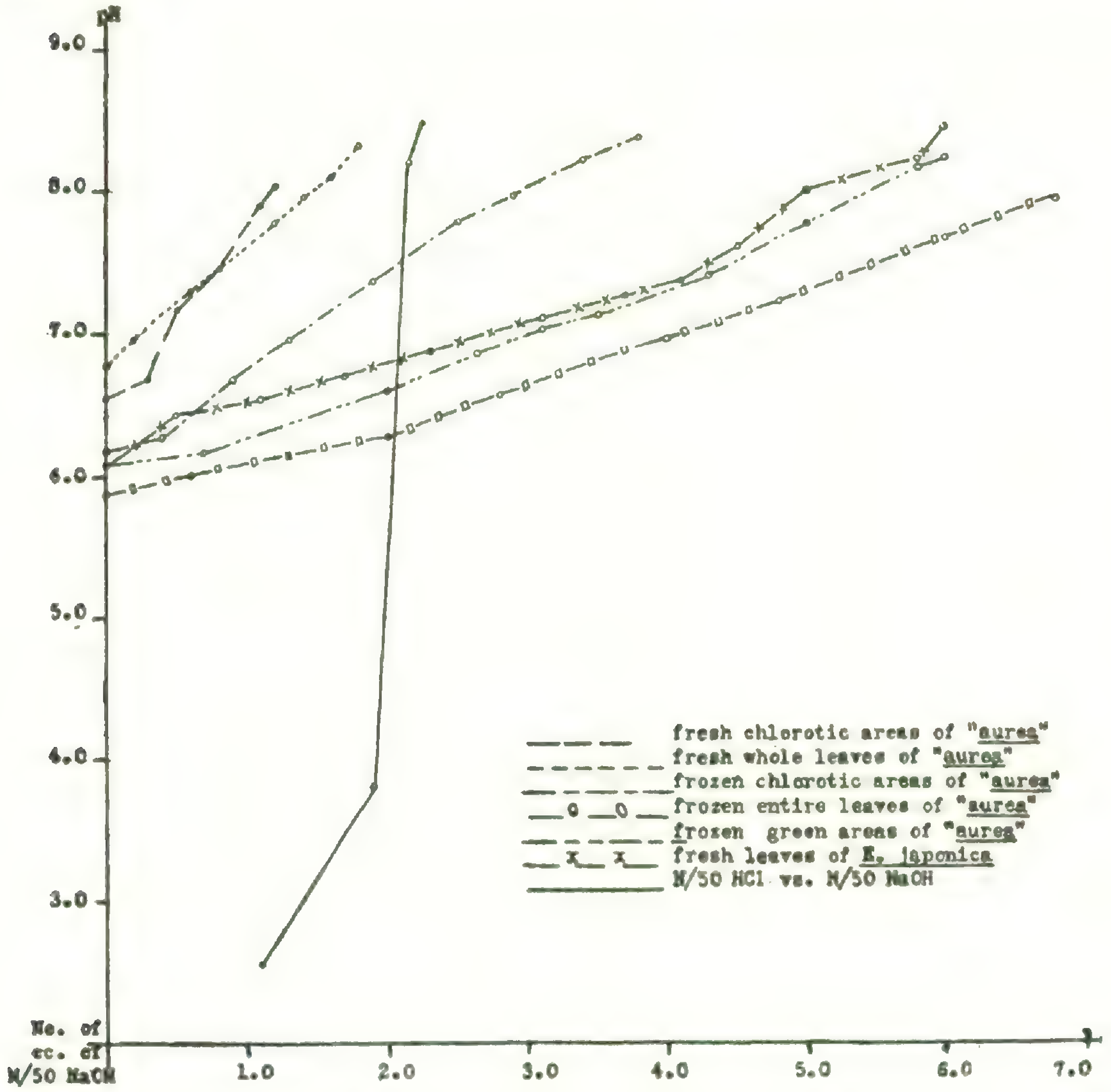


Fig. 2. Titrations of *E. japonica* var. "*aurea*" and of *E. japonica* with N/50 NaOH.

Similar experiments were conducted on variegated leaves of *E. japonica* "*medio-picta.*" The titrations were made with N/20 NaOH and in some cases with N/50 NaOH. Representative curves from the titrations with N/20 NaOH are shown in text-fig. 3.

Results.—The graphs in text-figs. 2 and 3 show that variegated varieties of *Evonymus japonica* group themselves into two distinct categories, namely, those exhibiting pronounced and prolonged buffer action, and those exhibiting less pronounced and prolonged buffer action. To the first category belong all titration curves

of juices expressed from frozen leaf tissue. To the second belong all titration curves of juices expressed from fresh or non-

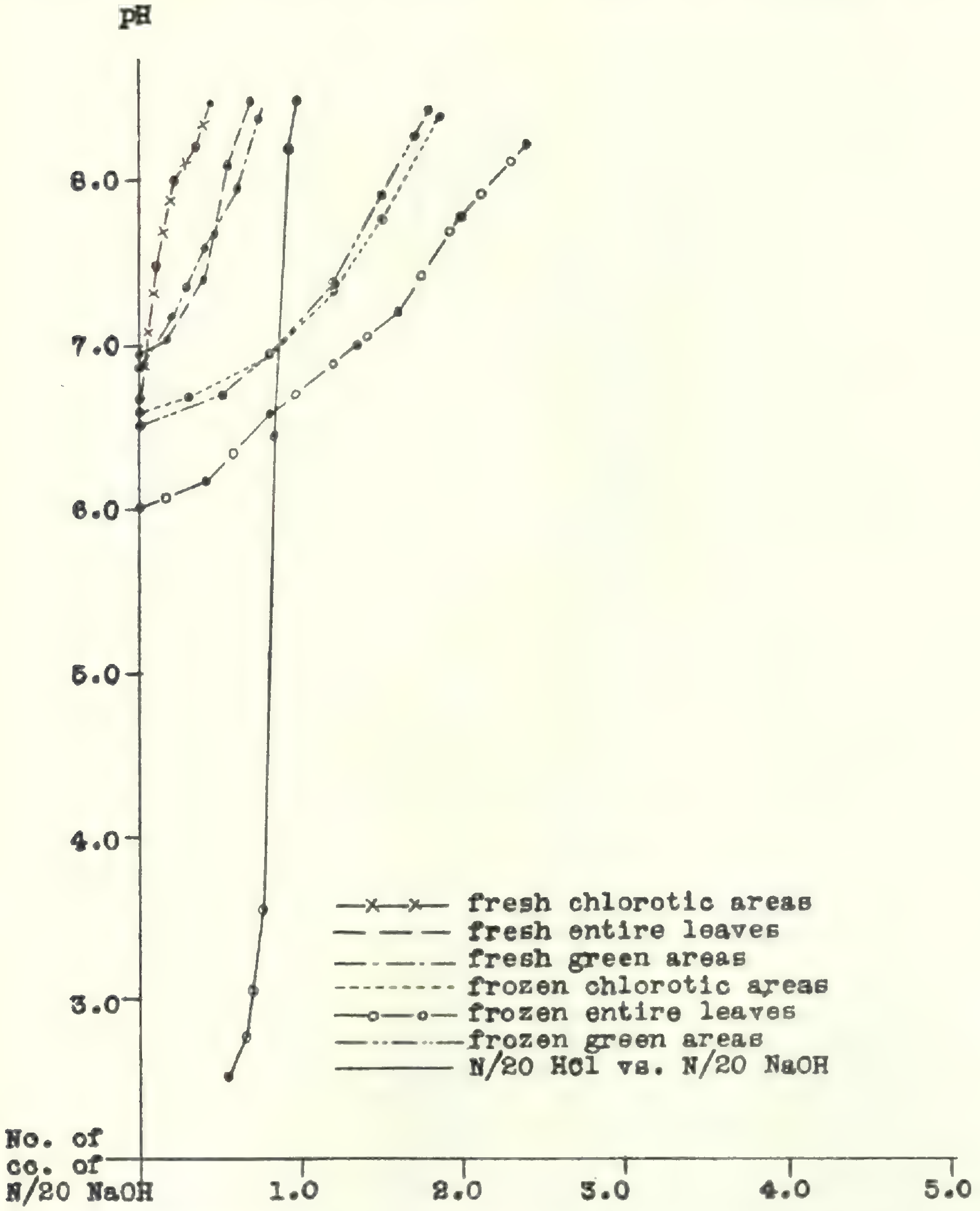


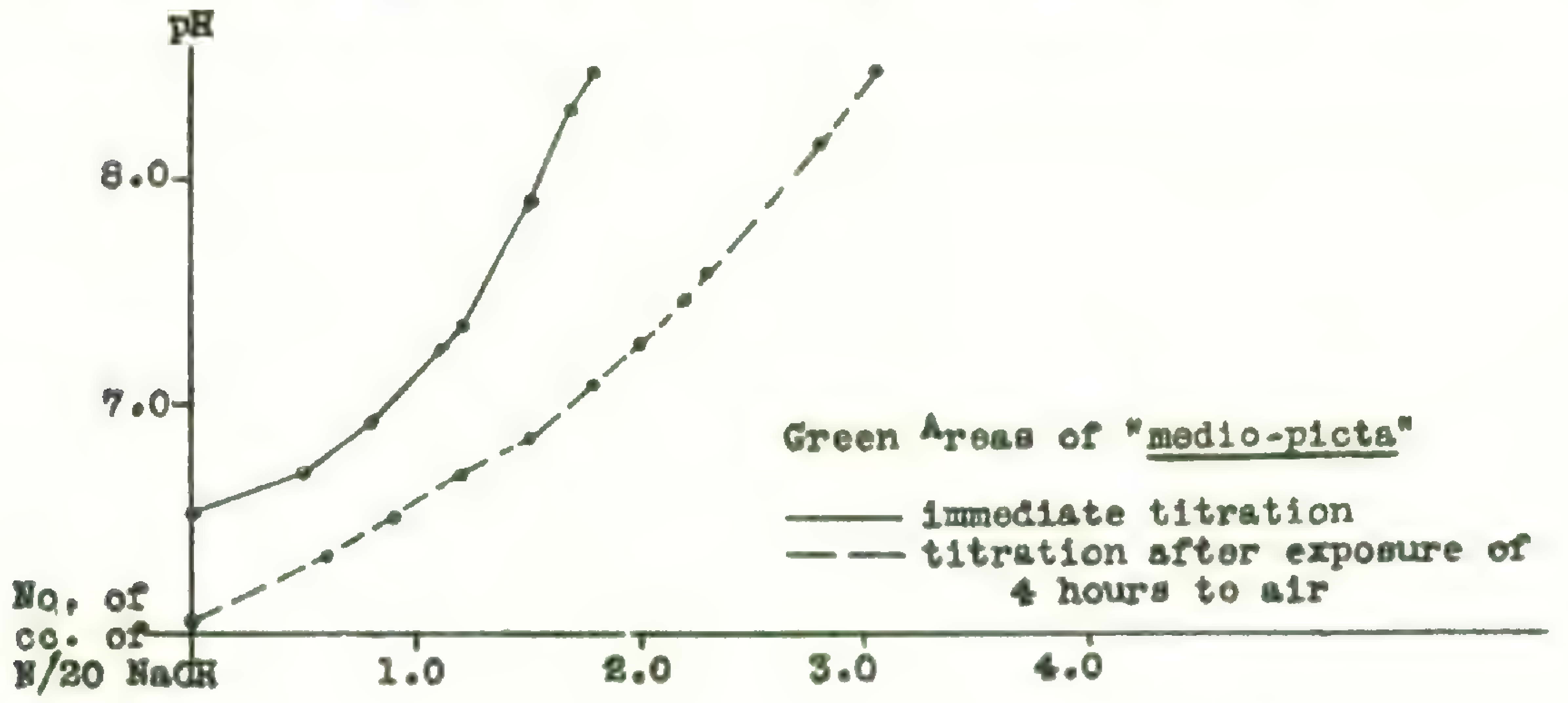
Fig. 3. Titrations of *E. japonica* var. "*medio-picta*" with N/20 NaOH.

frozen leaf tissue. Titration curves of the juices expressed from fresh leaves of the green variety fall into the first category along with curves for the titration of juices of frozen variegated leaves.

Many more titrations were made than were plotted here, without the occurrence of a single exception to the case in point.

EFFECT OF EXPOSURE OF EXPRESSED JUICE TO AIR

Method.—In this experiment part of the juice expressed from variegated and green leaves of *E. japonica* was titrated immedi-



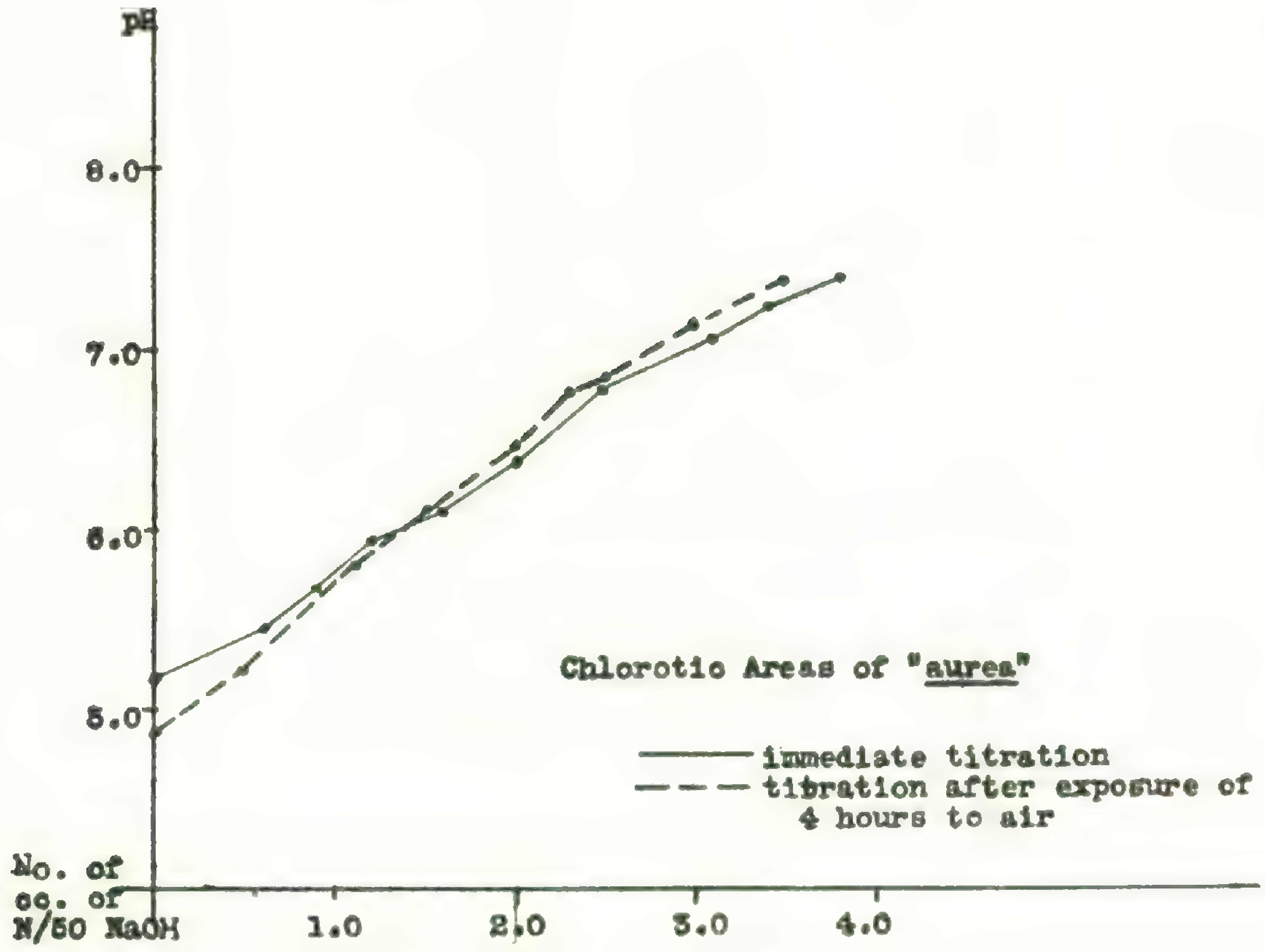


Fig. 4. Effect of exposure of expressed juice to air.

ately, while the other part was set aside and exposed to air for intervals of time varying from four to twelve hours, and then titrated.

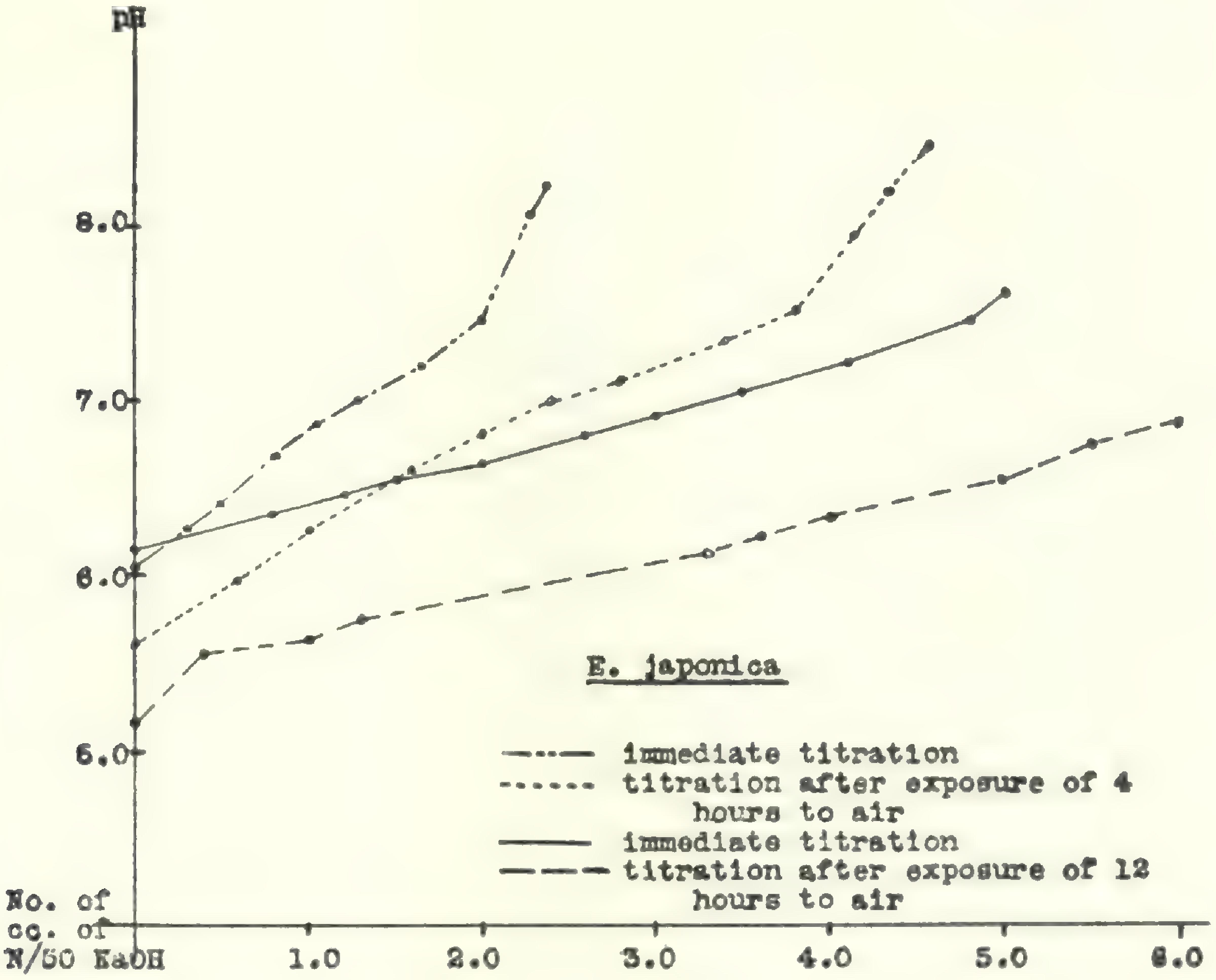


Fig. 5. Effect of exposure of expressed juice to air.

Results.—The initial acidity determinations as shown in text-figs. 4 and 5 all point to one conclusion, namely, that the juices from entire green leaves of the green variety and from the chlorotic and green portions of the leaves of the variegated varieties became more acid on standing in an atmosphere of air. It is clearly indicated on the graphs that a similar relationship also holds for the entire titration except in juices from chlorotic areas. That is to say, the curves, though not identical, run parallel; a fact which indicates that during the course of the titrations of the samples exposed to air for four to twelve hours there resulted a consistently lower pH when equal quantities of N/50 NaOH were added to samples from green areas. The author has no

data to show whether or not the same holds true for the entire leaves of variegated individuals.

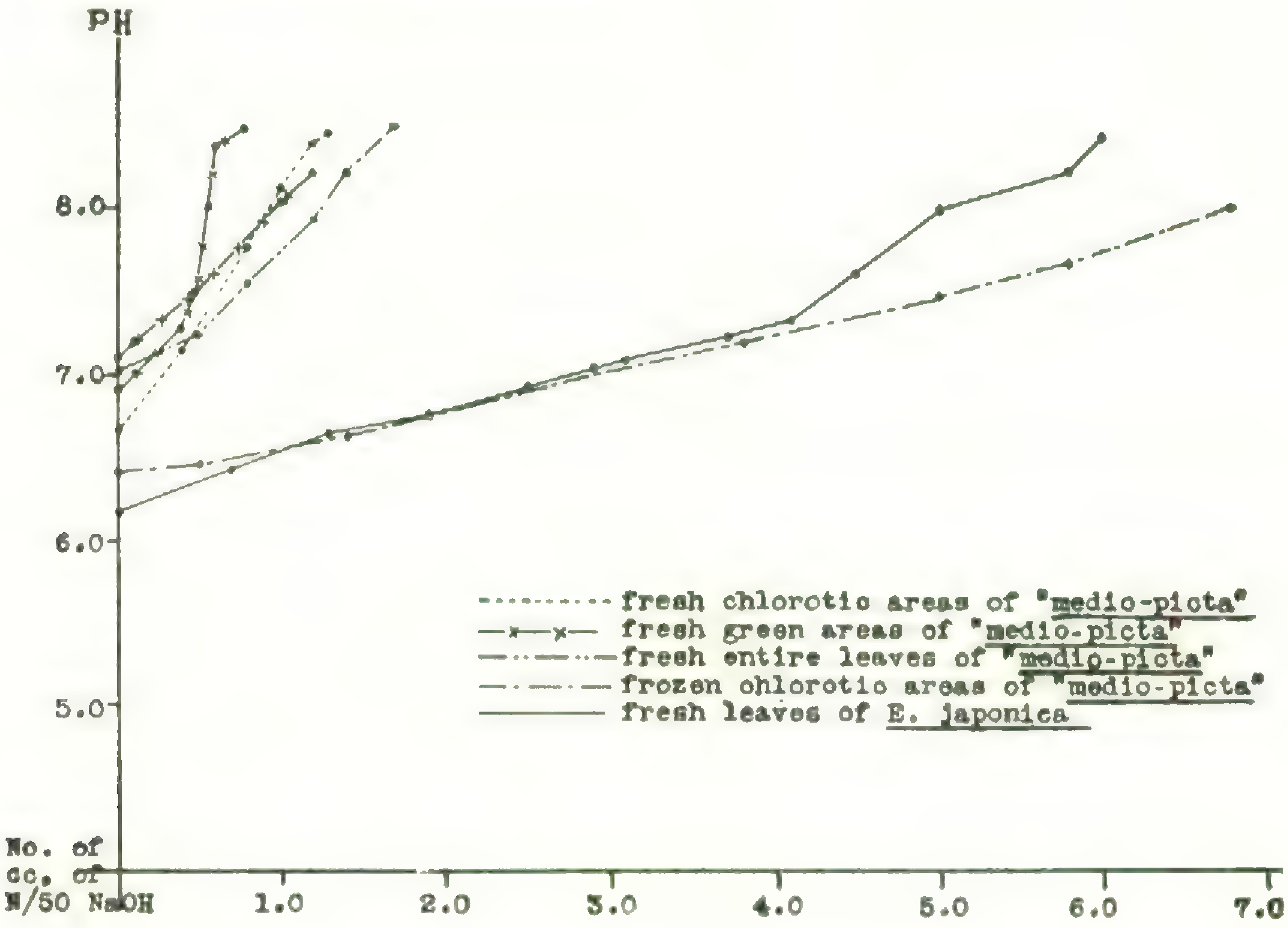


Fig. 6. Titrations of *E. japonica* var. "*medio-picta*" and of *E. japonica*.

Discussion

The data obtained from the foregoing experiments have a direct bearing upon the conclusions of certain earlier authors whose results were presented in the "Discussion of Literature" in this paper. From the author's own work and that of Baur, it is clear that the condition of mottling in infectious chloroses can be produced under light in both halves of the spectrum. The observations of Baur ('06a) with reference to the loss of the chlorotic appearance as a result of exposure of plants to light of various wave-lengths could not be substantiated in the case of *Evonymus japonica* var. "*aurea.*" Although the writer observed that leaves of *Abutilon Thompsonii* became quite uniformly green during the five-months exposure to sunlight deficient in blue rays under one set of conditions, and green rays under another, he is inclined to favor the view that these effects may be attributed partially or entirely to shade which was produced

under Corning's glasses Noviol "C" and G 34, as this factor could not be successfully eliminated during the winter months.

In considering further the influence which light may have on the expression of the infectious variegation, it might be argued that increased illumination and possibly continuous exposure to light of high intensity might favor the spread of the chlorotic condition of infectious chlorosis to all parts of the leaf. In so far as it can be ascertained from experiments of high-light intensity and from the continuous exposure of the infected plants to this intensity, there is no physiological factor in the infected leaves of *Abutilon Thompsonii* and *Evonymus japonica* var. "*aurea*" which can be influenced by light to cause them to become entirely and uniformly yellow through the enlargement of the chlorotic areas.

Plants of *A. Thompsonii* receiving light for five- and seven-hour day lengths, as compared with those grown under identical conditions except for exposure to longer periods of day length, developed new leaves, of which each successive crop became more uniformly green until new leaves matured which were entirely free from the chlorotic condition. Comparable results were obtained by Baur when plants of *A. Thompsonii* were partially shaded from sunlight. Where Baur's results were obtained from few plants held under experimental conditions which were unsatisfactorily controlled, the results from the present study were obtained by experimenting with a large number of plants held under carefully controlled conditions. It is interesting to note that shade and short-day length have similar effects on the infectious variegations.

Baur emphasized the curing effects which exposure to darkness had upon plants infected with chloroses. Results given in the present paper show that such treatment, for short periods of time at least, was not sufficient to destroy the infectious property of the virus, as was evidenced by the fact that after a plant was returned to the light the new leaves which formed promptly became infected. However, when the plants were kept in the dark after defoliation of the mature leaves, new and etiolated leaves were formed which developed chlorophyll when the plants were brought into the light, and these remained on the stem in the vicinity of subsequently formed variegated leaves

without becoming infected. The fact that leaves which are formed in the dark will remain uninfected although they mature in the light may possibly be explained by some such hypothesis as Baur's theory of immunity. He pictured a type of immunity which would explain the fact that if leaves were prevented from becoming infected until they had attained a certain degree of differentiation and development, they would thereafter remain immune to infection. A plant of *A. Thompsonii* kept in the light can be restored permanently to a condition where it is uniformly green by removing the variegated leaves for several successive crops. These facts have led the author to the conclusion that the curing effects observed by Baur which he attributed directly to the absence of light may be due principally to defoliation.

The greening processes of variegated leaves may possibly be related to the absence of normal metabolic and synthetic activities of the plants under investigation. Whether the infectious agency can be inactivated or made to lose its power of reproduction by means of certain light treatments, or, on the other hand, the leaf tissues rendered effectively resistant to the invasion of the virus by such treatments, can be subjected to experimental proof. In the light of such a test, it would become a point of theoretical interest to follow the changes in the chemical constituents related to the metabolism of the leaf and to the photosynthate for certain stages of the greening processes. This work will be carried out in the future as time permits.

When samples of juice expressed from green and chlorotic portions of leaves of varieties of *Evonymus japonica* were exposed to air, and the hydrogen-ion concentrations were determined upon these at intervals of time varying from a few minutes to several hours, it was found that an increase of acidity of the juice was proportional to time. The author has been unable to attach any theoretical significance to the linear nature of the pH curves from the present data, or to account satisfactorily for the rapid fall of pH with time. The failure to transmit infectious chlorosis by other means than by grafting or budding makes it important to consider any changes that may be detected in the juices from the time that the macerated leaf tissue is exposed

to the air to the moment that inoculation is made into the susceptible green plant. Therefore, such changes in the hydrogen-ion concentration should be prevented, as far as possible, during inoculation experiments in cases where the inoculum ordinarily fails to transmit the infectious virus. Acidity experiments performed by Dr. B. M. Duggar, but not reported, showed a similar phenomenon in chlorotic and green areas of plants infected with true mosaic disease.

From results of electrometric titration experiments on juices of frozen and non-frozen leaves of varieties of *Evonymus japonica*, it can be concluded that freezing has increased buffer action in the juices expressed from these varieties. The data suggest the possibility that cells may be ruptured by the freezing process, with the result that the cell contents may be expressed more completely from the pulp under hydraulic pressure. Titration curves of data from experiments in which the titrations were made after the juices were allowed to stand in an atmosphere of air show a consistently lower pH when equal quantities of N/50 NaOH were added to samples from green areas. It is considered likely that a process of organic oxidation may be concerned here. Carbohydrates may be oxidized to form organic acids, a result which would bring about an increase in acidity which would be consistent with the data from similarly performed experiments with expressed juices where the free and the titratable acidities have been determined simultaneously.

There are certain contrasts in buffer action between variegated and green leaves of *Evonymus japonica* which have been clearly brought out by the foregoing experiments. From the data which have been presented here, it can be assumed that the tissues in yellow and green portions of variegated leaves exhibit distinctiveness in regard to the nature of their physiological processes. Additional evidence pointing to the same conclusion is not lacking from data of other titration experiments. This evidence will be briefly summarized in the following paragraphs.

Juices from the fresh or non-frozen variegated leaves of varieties *E. japonica* "*medio-picta*" and "*aurea*" show relatively little buffer action as compared with the juice from leaves of the green variety (see text-figs. 3 and 6).

The juices from frozen variegated leaves show a significant increase in buffer action over and above that for juice from fresh leaves. The curves for the titrations of juice from the frozen variegated leaves are strikingly similar to those for the juice from fresh leaves of the green variety.

In the case of the titrations of fresh leaves of "*medio-picta,*" of which representative curves are shown in text-fig. 6, there is some indication that buffer action is least in chlorotic areas and greatest in entire leaves; the curves for green areas and entire leaves, however, were similar. This difference is not evident in titrations of fresh leaves of "*aurea.*" This may be due to the fact that only three titrations were made of fresh material in the latter case.

Smith ('26) has observed that the invisible rays of ultra-violet light from a quartz mercury vapor lamp caused a masking of the chlorotic symptoms on tobacco plants infected with true mosaic disease. It would be of interest to subject *Abutilon Thompsonii* to ultra-violet radiations through a series of glass filters the transmissions of which are known.

There have been no experiments recorded, in the literature or in the present study, to determine whether or not mottling on the leaves of *Abutilon* bears any direct relation to temperature. This subject has received the attention of physiologists dealing with tobacco and potato mosaics, and hence would be of interest in connection with these studies.

Baur's attempts to grow variegated plants of *Abutilon* in an atmosphere of air in which the carbon dioxide had been removed should be repeated in such a way as to permit a carbon dioxide-free air to be circulated and constantly renewed.

Summary

1. The observations of Baur ('06a) with reference to the effects which the quality of light had upon certain plants infected with chlorosis could not be confirmed in the case of *Evonymus japonica* var. "*aurea.*" While the leaves of plants of *Abutilon Thompsonii* were observed to become quite uniformly green during the five-months exposure to sunlight deficient in blue rays under one set of conditions and green rays under another, the author is inclined

to favor the view that these effects may be attributed partially or entirely to shade which was produced under Corning's glasses Noviol "C" and G 34.

2. Continuous illumination for two months under experimentally controlled conditions where the intensity of light closely approached that of sunlight throughout the duration of the experiments, did not materially or permanently alter the typical variegated appearances of *Abutilon Thompsonii, Evonymus japonica* vars. "*aurea*" and "*medio-picta*" as compared with similar plants held under usual greenhouse conditions for the same interval of time. *Abutilon Thompsonii* plants receiving short exposures to artificial light under controlled conditions such as five-hour day and seven-hour day for an equal period of two months were observed to develop new leaves which became successively more uniformly green. Near the end of the experiments new leaves were maturing entirely without a chlorotic condition. It is possible that this should be said with some reservation, as here and there very minute chlorophyll-free specks, just visible to the unaided eye, could be observed on some leaves, which specks did not appear on control plants with uniformly green leaves when they were first placed under the conditions of the short-day experiments. Photographs showing these different effects are included in pl. 9.

3. Exposures of plants of *A. Thompsonii* to total darkness for intervals of time varying from several days to two weeks, during which time the stems became entirely defoliated of mature leaves resulted in the total loss of variegation in new leaves which were formed while the plants were in the dark, but matured in the light. On the other hand, leaves which developed after the plants were restored to the light became infected.

4. Studies of *Abutilon Thompsonii* made upon fixed and stained sections of areas transitional between green and chlorotic regions of strongly variegated leaves show little contrasting differentiation. No X-bodies were found in chlorotic, green, or transitional areas of the variegated leaves. Light treatments resulted in striking morphological modifications in leaf structure.

5. All attempts have failed to transmit the infectious chloroses by any other means than by grafting.

6. Successful transmission was obtained by grafting and budding *Evonymus japonica* var. "*aurea*" with green *Evonymus japonica.*

7. By stripping off successive crops of variegated leaves, *Abutilon Thompsonii* plants were made to develop uniformly green leaves, thus substantiating the work of Baur ('06a).

8. Electrometric determinations of hydrogen-ion concentrations were made by the quinhydrone electrode method, modified to accommodate determinations made in single drops of expressed juice, on crushed leaves of *Evonymus japonica* vars. "*aurea,*" "*argenteo,*" and "*medio-picta,*" as well as leaves of a green variety. The method was found accurate within .03 pH. The following results were obtained: Chlorotic areas of all variegated varieties except "*aurea*" were higher in initial acidity than were the green areas. It has been observed that the decrease in pH of juice expressed from both chlorotic and green areas is in general directly proportional to the time in minutes of exposure of the juice to air. Such changes appear to be of sufficient magnitude to warrant their consideration in attempts to transmit the chlorosis of *Evonymus* by other means than grafting.

9. Electrometric determinations of total acidity were made on juice from these tissues by an apparatus which would permit the accurate titration of 2-cc. quantities. It was found that freezing the leaves before expressing the juice caused increase in buffer action of juices from green and variegated varieties of *Evonymus.* Freezing the tissue should be guarded against in inoculation experiments. There was a pronounced increase in total acidity of samples taken from the leaves of the green variety and from the green areas of the variegated leaves but not of samples taken from the chlorotic areas, when the expressed juice was exposed to air for four to twelve hours. It is believed that this difference between the behavior of the green and chlorotic areas has a theoretical significance.

Acknowledgments

The writer wishes to express his sincere appreciation to Doctor B. M. Duggar for suggesting the problem and for his many helpful criticisms throughout the work; to Doctor G. T. Moore for the

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Bibliography

Baur, E. ('04). Zur Aetiologie der infektiösen Panachierung. Ber. d. deut. bot. Ges. **22**: 453–460. 1904.

————, ('06a). Weitere Mitteilungen über die infektiöse Chlorose der Malvaceen und über einige analoge Erscheinungen bei Ligustrum und Laburnum. *Ibid.* **24**: 416–428. 1906.

————, ('06b). Über die infektiöse Chlorose der Malvaceen. K. Preuss. Akad. Wiss. Sitzungsber. **1906**: 11–29. 1906.

————, ('07). Über infektiöse Chlorosen bei Ligustrum, Laburnum, Fraxinus, Sorbus und Ptelea. Ber. d. deut. bot. Ges. **25**: 410–413. 1907.

————, ('08). Über eine infektiöse Chlorose von Evonymus japonicus. *Ibid.* **26**: 711–713. 1908.

Beijerinck, M. W. ('99). Versammlung und zugleich Jahresversammlung des Vereins zur Beförderung des Gartenbaues am 29 Juni, 1899. Gartenflora **48**: 369–372. 1899.

Bouché, C. ('71). Ueber das Buntwerden der Blätter als krankhafte Antsteckung durch Pfropfreiser bei Evonymus japonicus, wie bei Abutilon. Ges. naturforsch. Freunde Berlin, Sitzungsber. **1871**: 66–68. July, 1871.

Bradley, (1726). A general treatise of husbandry and gardening, etc. p. 282. London, 1726.

Clark, W. M. ('20). The determination of hydrogen ions. 317 pp. Baltimore, 1920.

Elmer, O. H. ('25). Transmissibility and pathological effects of the mosaic disease. Iowa Agr. Exp. Sta. Res. Bull. 82: 39–91. *f. 2.* 1925.

Findlay, A. ('20). Practical physical chemistry. 327 pp. New York, 1920.

Funaoka, S. ('24). Beiträge zur Kenntnis der Anatomie panaschierter Blätter. Biol. Zentralbl. **44**: 343–384. *f. 1–13.* 1924.

Gale, A. S., and Watkeys, C. W. ('20). Elementary functions and applications. 436 pp. New York, 1920.

Grandsire, A. ('26). Lechemisme des feuilles privées de chlorophyll. Ann. Sci. Nat. Bot. X. **8**: 221–296. 1926.

Guthrie, J. D. ('28). A stable colorimetric standard for chlorophyll determinations. Am. Jour. Bot. **15**: 86–87. 1928.

Hein, I. ('26). Changes in plastids in variegated plants. Torrey Bot. Club, Bull. **53**: 411–418. *pl. 17.* 1926.

Hildebrand, J. H. ('13). Some applications of the hydrogen electrode in analysis, research and teaching. Am. Chem. Soc. Jour. **35**: 847–871. 1913.

Küster, E. ('27). Anatomie des panaschierten Blattes. Handbuch der Pflanzenanat. II. Abt. 2 Teil, **8**: 1–68. *f. 1–54.* 1927.

Lakon, G. ('16). Über die jährliche Periodizität panachierter Holzgewächse. Ber. d. deut. bot. Ges. **34:** 639–648. *f. 1–3.* 1916.

————, ('17). Über die Festigkeit der Ruhe panachierter Holzgewächse. *Ibid.* **35:** 648–652. *f. 1.* 1917.

Lawrence, J. (1715). The clergyman's recreations. p. 65. London, 1715.

Lemoine, J. F. ('69). Letter addressed to M. Duchartre. Soc. Imp. et. Centr. d'Hort. Fr., Jour. II. **3:** 47. 1869.

Lindemuth, H. ('72). Impfversuche mit buntblättrigen Malvaceen. Bot. Ver. Prov. Brandenburg, Verhandl. **14:** 32–37. *pl. 2.* 1872.

————, ('78). Über vegetative Bastarderzeugung durch Impfung. Landwirtsch. Jahrb. **7:** 887–939. *pl. 28–31.* 1878.

————, ('99a). Kitaibelia vitifolia Willd. mit goldgelb marmorierten Blättern. Gartenflora **48:** 431–434. *pl. 70.* 1899.

————, ('99b). Versammlung des Vereins zur Beförderung des Gartenbaues am 26. Oktober 1899. *Ibid.* 597–598. 1899.

————, ('02a). Über einige neue Pfropfversuche und Resultate. Ibid. **51:** 12–15. 1902.

————, ('02b). Vorläufige Mitteilungen über weitere Impfversuche an Malvaceen Arten. *Ibid.* 323–326. 1902.

————, ('07). Studien über die sogenannte Panaschüre und über einige begleitende Erscheinungen. Landwirtsch. Jahrb. **36:** 807–861. *pl. 8–9. f. 1–16.* 1907.

Masters, M. T. ('69). Vegetable teratology. 534 pp. London, 1869.

Morren, E. ('69). Contagion de la panachure (Variegatio). Acad. Roy. Belg. Bull. II. **28:** 434–442. *1 pl.* 1869.

Pantanelli, E. ('05). Über Albinismus im Pflanzenreich. Zeitschr. f. Pflanzenkrankh. **15:** 1–20. 1905.

Rischkow, W. ('27a). Einige neue wildwachsende buntblättrige Pflanzen. Biol. Zentralb. **47:** 18–25. *f. 1.* 1927.

————, ('27b). Neue Daten über geaderte Panaschierung bei Evonymus japonicus and E. radicans. *Ibid.* **47:** 752–764. 1927.

Sageret, ('69). Inst. Hort. Fromont, Ann. **6:** p. 332. 1869.

Schertz, F. M. ('21). A chemical and physiological study of mottling of leaves. Bot. Gaz. **71:** 81–130. *f. 1–6.* 1921.

Smith, F. F. ('26). Some cytological and physiological studies of mosaic diseases and leaf variegations. Ann. Mo. Bot. Gard. **13:** 435–484. *pl. 13–16. f. 1–4.* 1926.

Tsinen, S. J. ('23). Recherches histologiques et cytologiques sur la panachure dans le genre Abutilon. Soc. Sci. Nancy Bull. IV. **2:** 25–26. 1923. [Abstr. in Bot. Abstr. **14:** 8434. 1925].

————, ('24). Recherches sur l'histologie des plantes panocliées et sur le mécanismes cytologique de la panachure. Thèse Univ. Nancy. 104 pp. *13 pls. 10 f.* 1924.

Vinson, C. G. ('27). Precipitation of the virus of tobacco mosaic. Science N. S. **66:** 357. 1927.

Willstätter, R., and Stoll, A. ('13). Untersuchungen über Chlorophyll. 424 pp. *16 f.* Berlin, 1913.

————, ('18). Untersuchungen über die Assimilation der Kohlensäure. 448 pp. *16 f.* Berlin, 1918.

Woods, A. F. ('99). The destruction of chlorophyll by oxidizing enzymes. Centralbl. f. Bakteriol., 2 Abt. **5**: 745–754. 1899.

Zimmerman, A. ('92). Ueber die Chromatophoren in panachierten Blättern. Beiträge zur Morphologie und Physiologie der Pflanzenzelle **1**: 80–111. Tübingen, 1892.

Explanation of Plate

PLATE 5

Semi-diagrammatic camera-lucida drawings of cross-sections of leaves of *A. Thompsonii*, showing the effect of light treatment.

Fig. 1. Condition after fourteen days of the experiment. Notice increased size of cells, spaces, thickness of leaf section, and abundance of chloroplasts. Continuous illumination of sunlight and gantry crane.

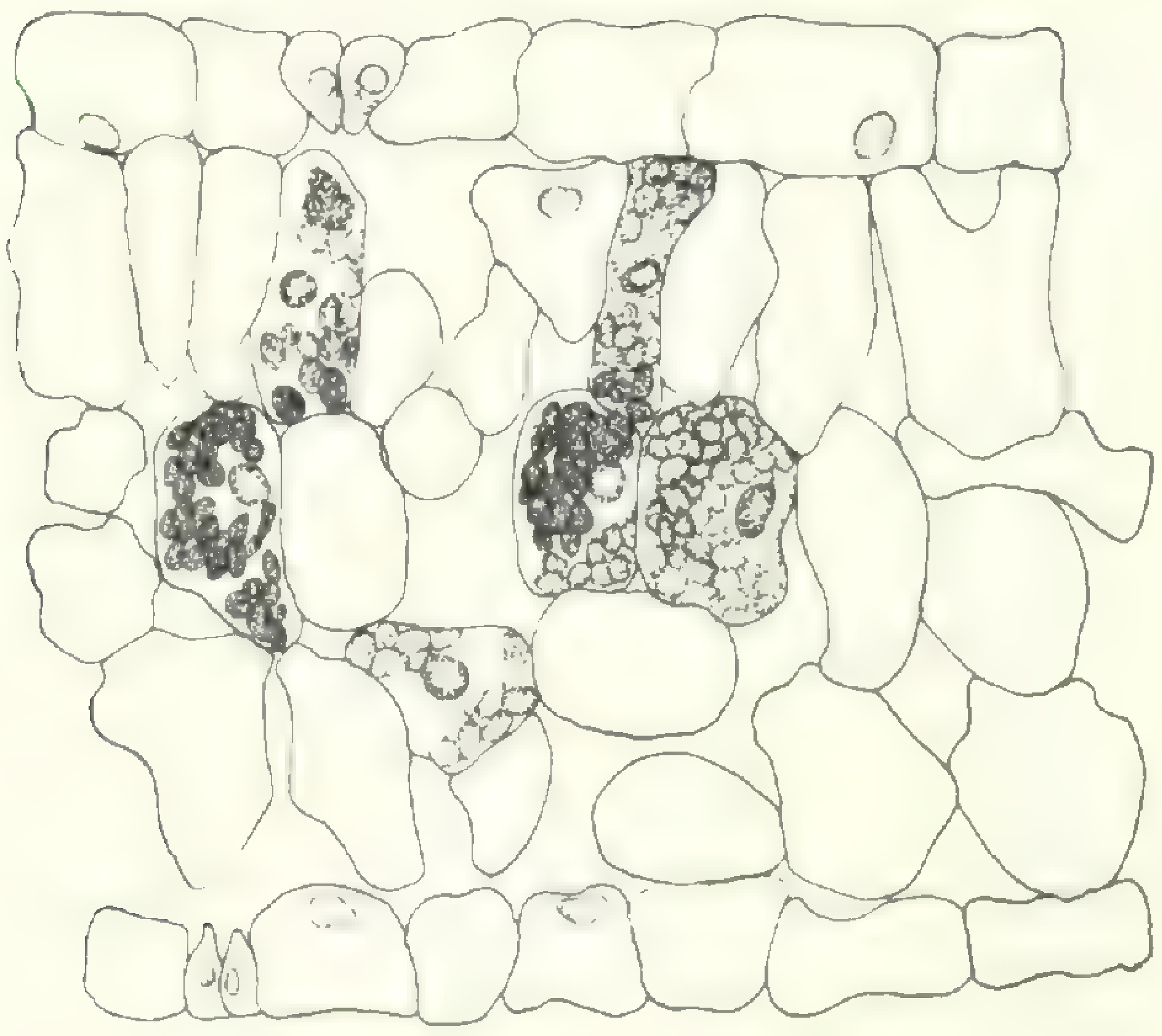
Fig. 2. Condition at beginning of experiment. Notice presence of unusually large intercellular spaces. Continuous illumination of sunlight and gantry crane.

Fig. 3. Chlorotic area at beginning of experiment. Continuous artificial illumination.

Fig. 4. Green area (?) of leaf drawn from same section as used in fig. 3.

Fig. 5. Condition at beginning of experiment, five-hour day.

Figs. 6 and 7. Condition fourteen days later, five-hour day. Notice modifications as opposed to those under continuous illumination.



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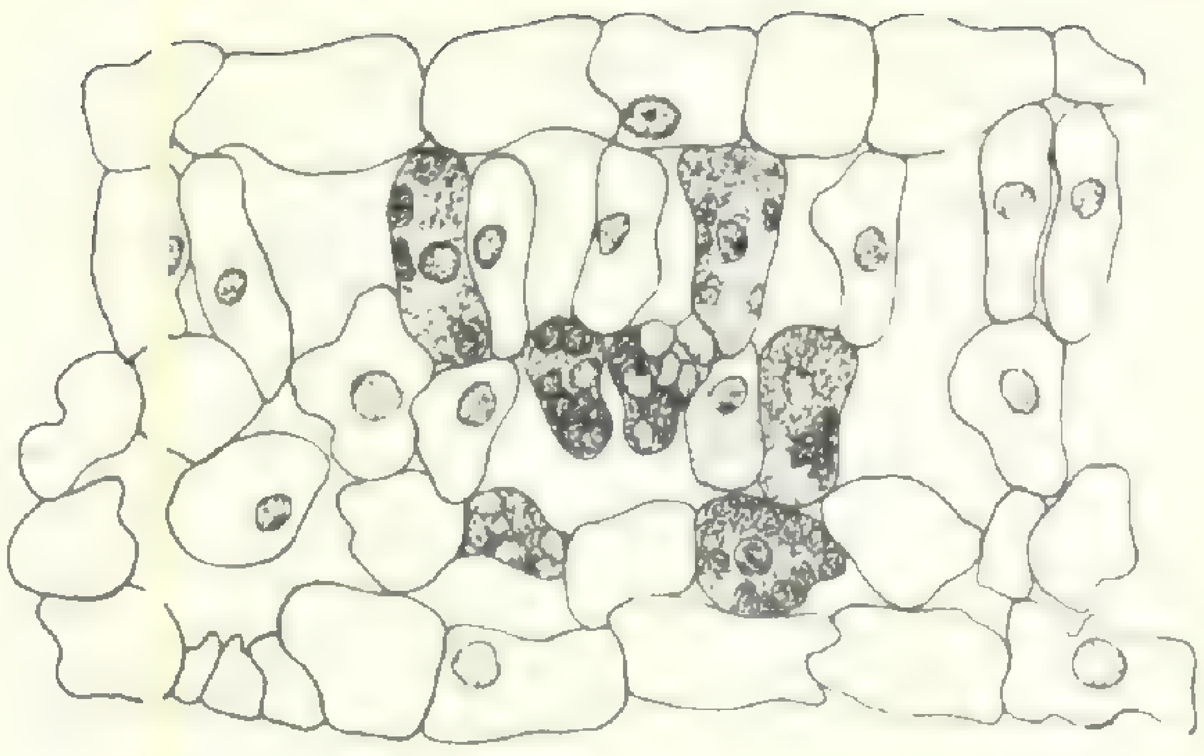

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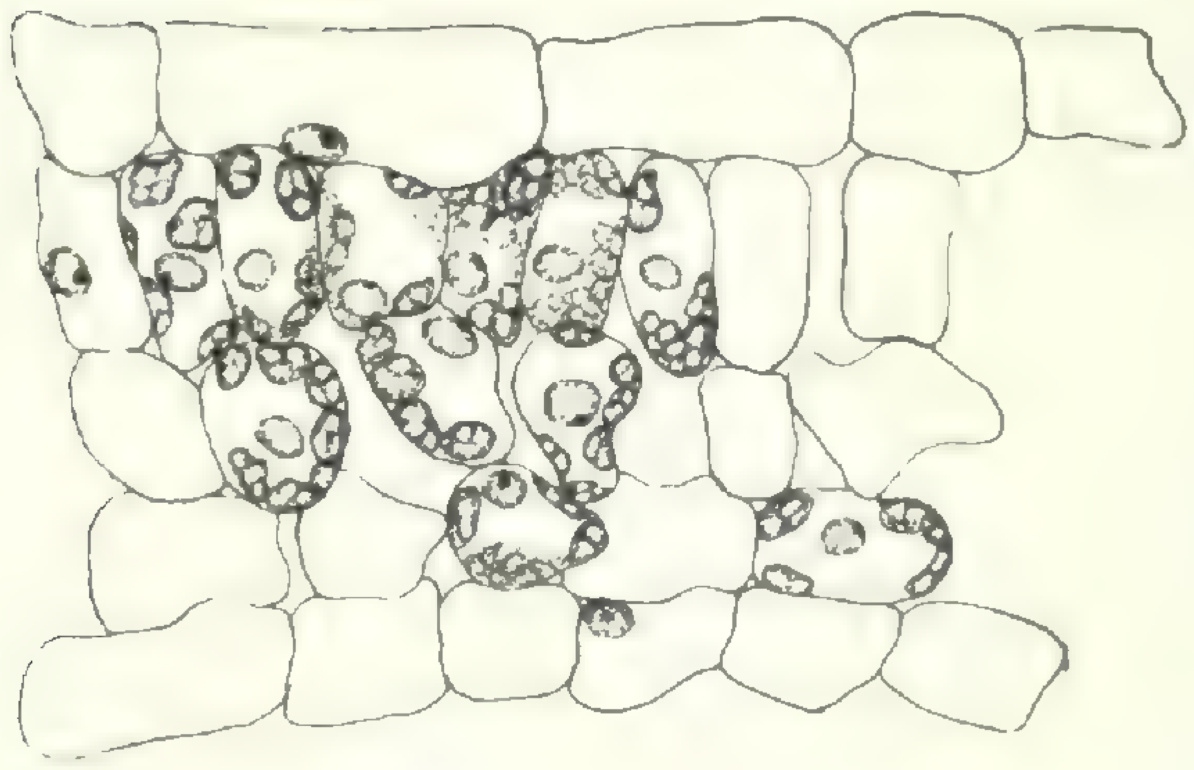

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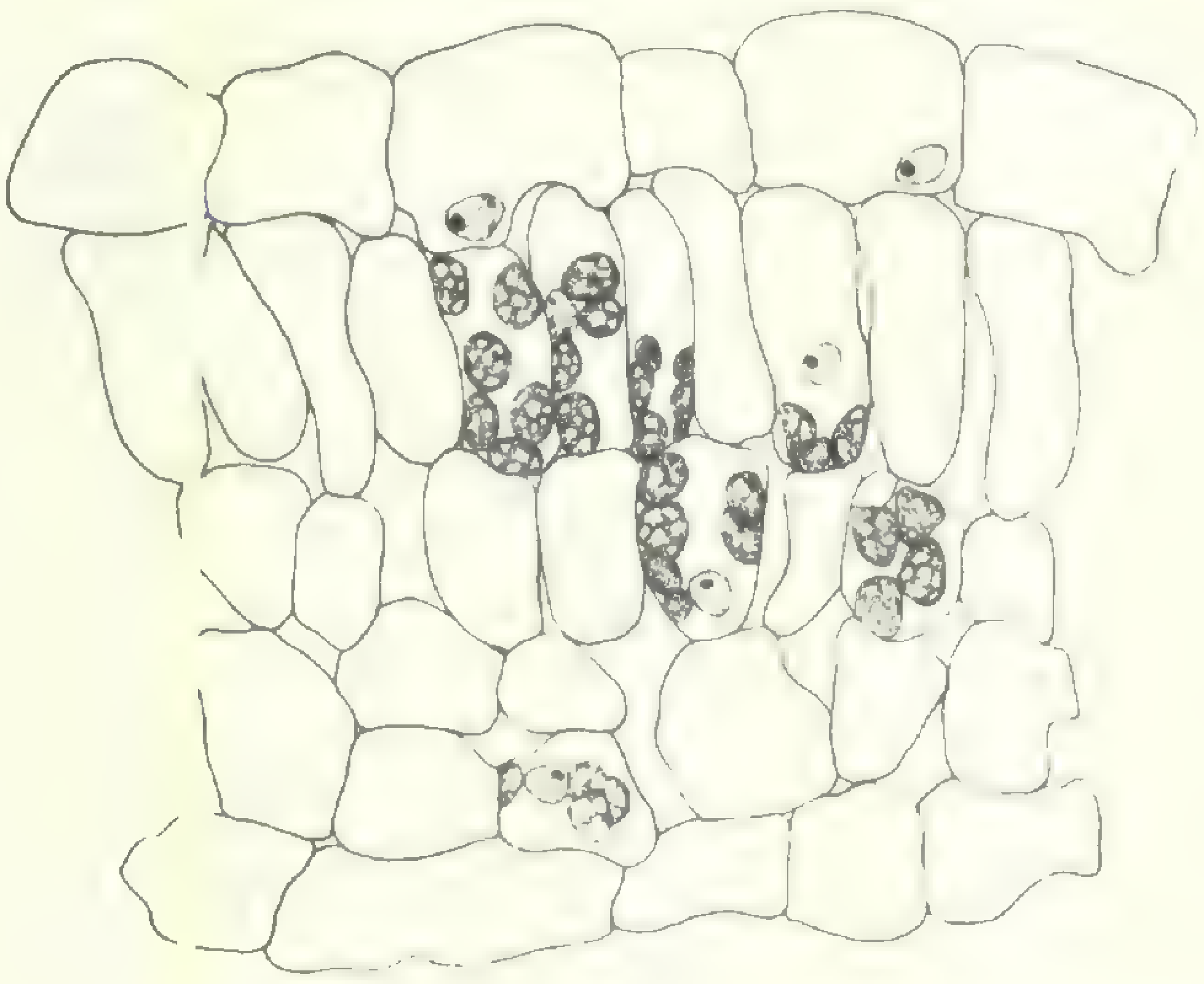

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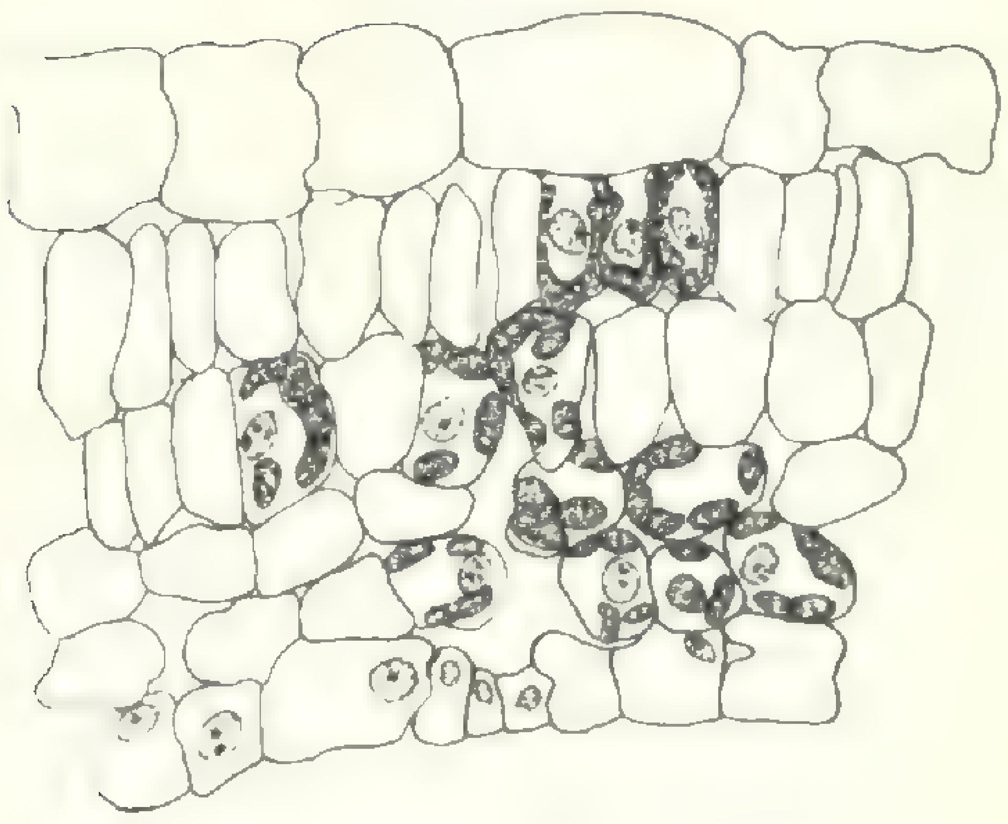

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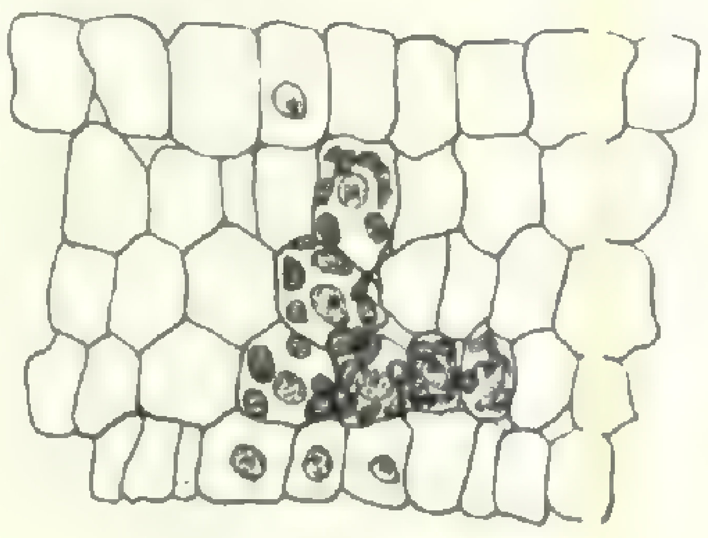

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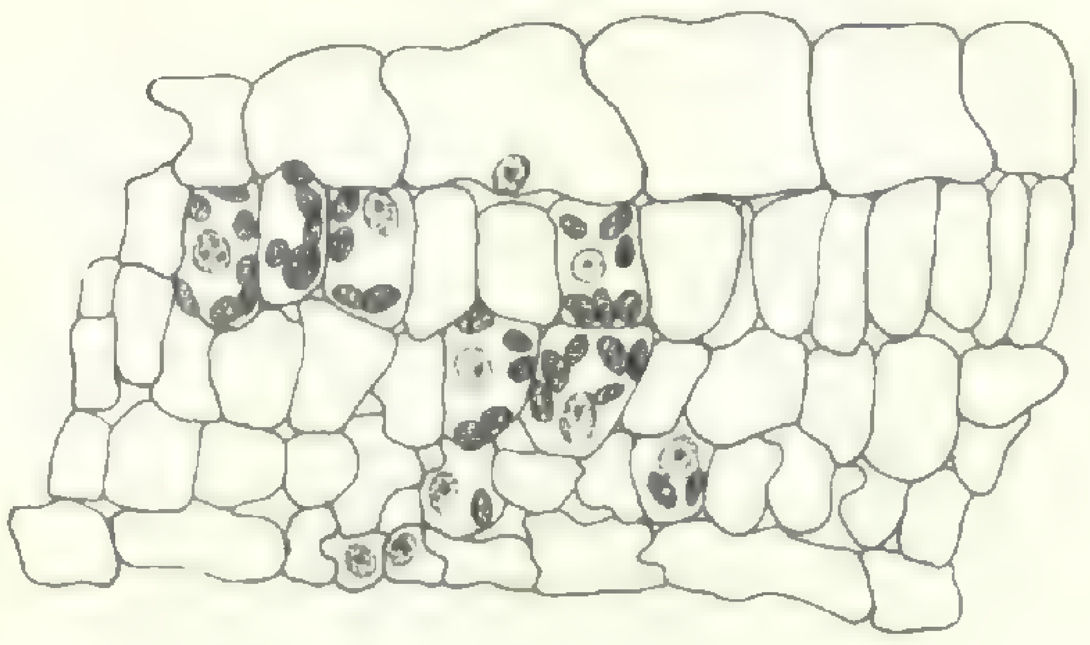


7

DAVIS—INFECTIOUS CHLOROSIS

Explanation of Plate

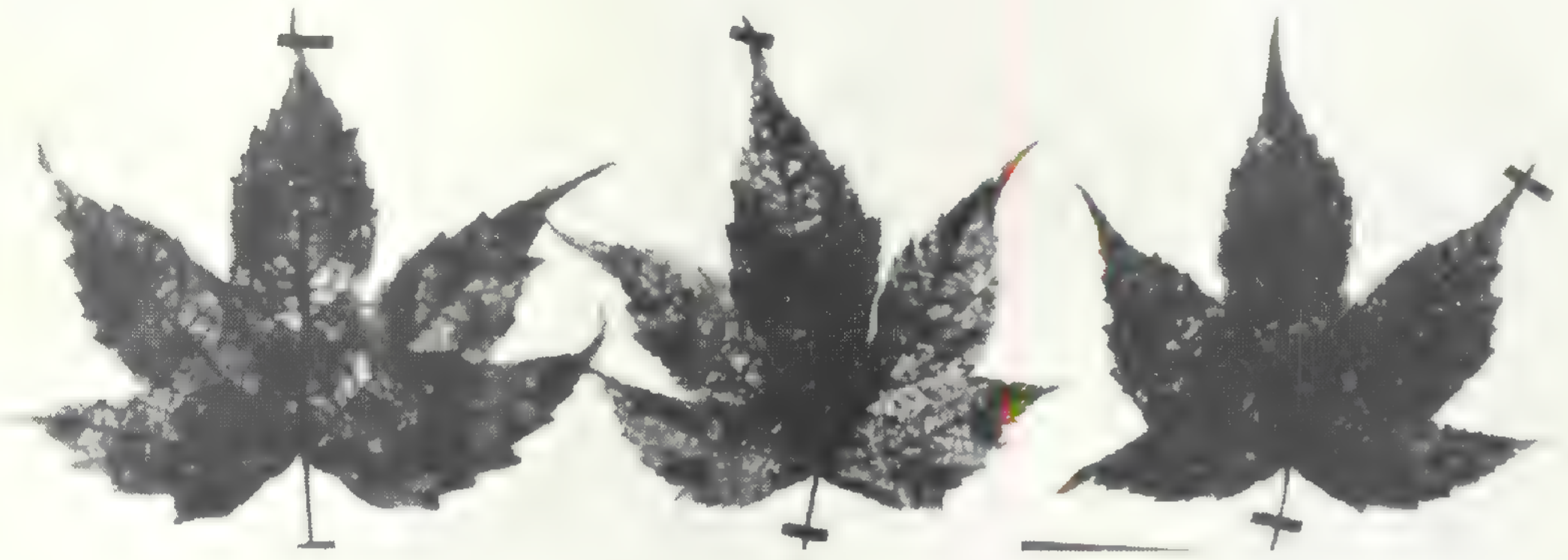
PLATE 6

Fig. 1. Plants of *Abutilon striatum* var. *Thompsonii*, variegated at beginning of experiment on light.

Fig. 2. Variegated leaves of *Abutilon Thompsonii*, showing typical mosaic pattern resulting from infectious chlorosis. Notice that the larger veins as well as some of the smaller ones limit the extent of the chlorotic areas.

Fig. 3. Variegated plants of *Evonymus japonica* at beginning of experiment on light.

1



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DAVIS—INFECTIOUS CHLOROSIS

Explanation of Plate

PLATE 7

Fig. 1. New leaves of *A. Thompsonii*, showing effect of continuous artificial illumination for ten days, compared with leaves from control plants.

Top, left to right: 1, 1-ranked leaf from control plant; 2, 2-ranked leaf from control plant; 3, 1-ranked leaf under continuous artificial illumination after ten days; 4, 2-ranked leaf under continuous artificial illumination after ten days.

Bottom, left to right: 1, 1-ranked normal green leaf; 2, 2-ranked normal green leaf; 3, 1-ranked leaf under continuous artificial illumination after ten days; 4, 2-ranked leaf under continuous illumination after ten days.

Fig. 2. Showing transmission of infectious chlorosis by grafting experiments: 1, *Abutilon Thompsonii*, variegated; 2, *Kitaibelia vitifolia*, green; 3, *Kitaibelia vitifolia*, variegated, showing infection through grafting. (After Lindemuth ('99a), fig. 70).

Fig. 3. Showing transmission of infectious chlorosis by grafting experiments: *Althaea rosea* root graft in union with the stem of *Abutilon Thompsonii*, from which it became infested with chlorosis. (After Lindemuth ('07), fig. 50).

DAVIS—INFECTIOUS CHLOROSIS

Explanation of Plate

PLATE 8

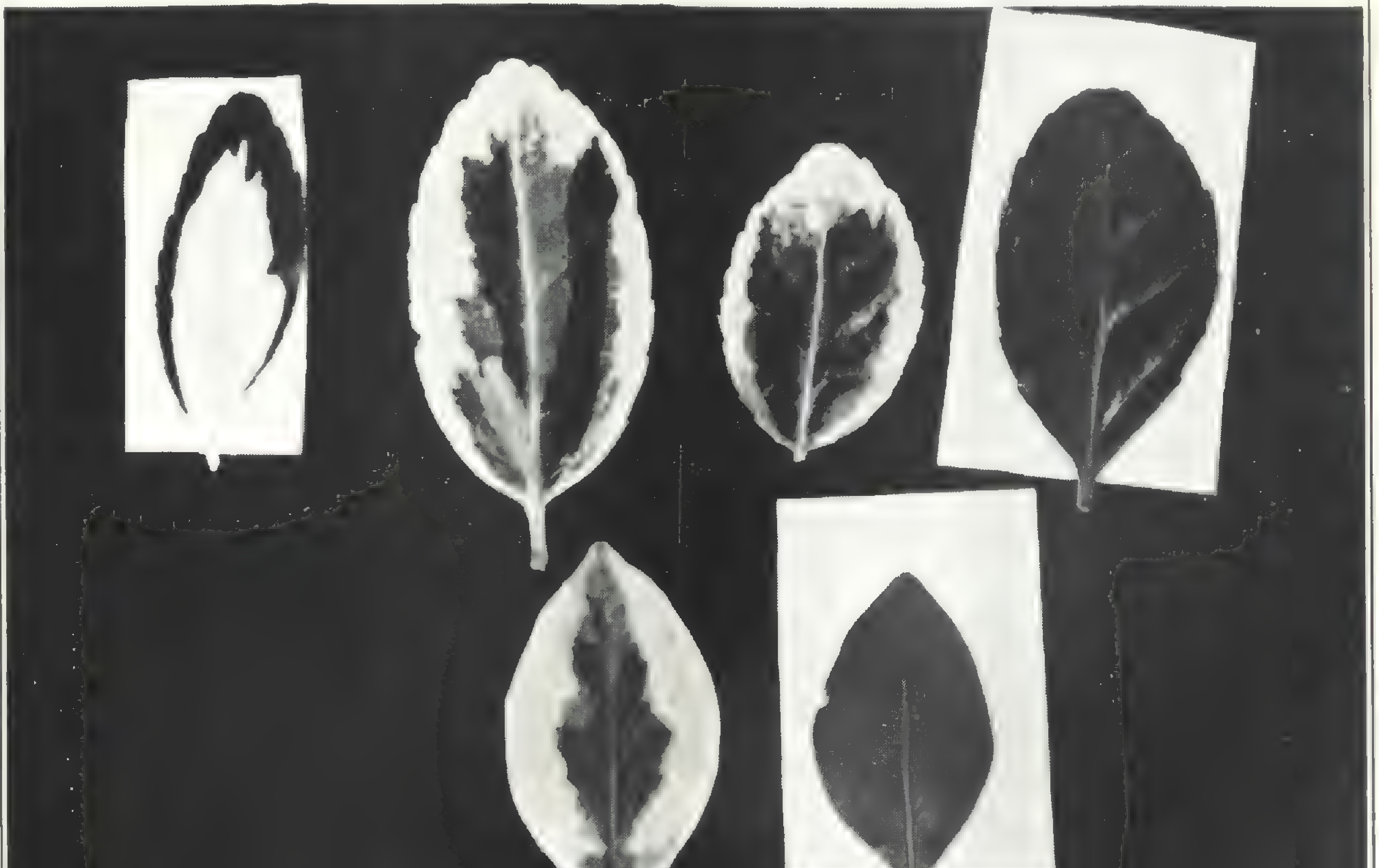
Fig. 1. *Abutilon megapotamicum* showing infectious chlorosis.

Fig. 2. Variegated leaves of *Evonymus japonica* varieties.

Top, left to right: 1, *E. japonica* var. "*medio-picta*"; 2 and 3, *E. japonica* var. "*argenteo*"; 4, *E. japonica* var. green.

Bottom, left to right: 1, *E. japonica* var. "*aurea*"; 2, *E. japonica* var. green.

1



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Explanation of Plate

PLATE 9

Fig. 1. *Abutilon Thompsonii*, showing effects of five-hour-day treatment.
Left to right: 173, *Abutilon* var. green, not infected; 28, 19, 8, 25, *Abutilon Thompsonii* variegated, showing loss of variegation among top leaves which developed during two months five-hour-day treatment; 120, 12, *Abutilon Thompsonii*, variegated, as they were under ordinary greenhouse conditions.

Fig. 2. *Abutilon Thompsonii*, showing effects of seven-hour-day treatment.
Left to right: 169, *Abutilon* var. green, from control greenhouse, not infected; 124, 94, 45, 120, *Abutilon Thompsonii* variegated, showing some loss of variegation among top leaves which developed during two months seven-hour-day treatment; 12, *Abutilon Thompsonii* variegated as in the control greenhouse; 173, *Abutilon* var. green, from control greenhouse.

1

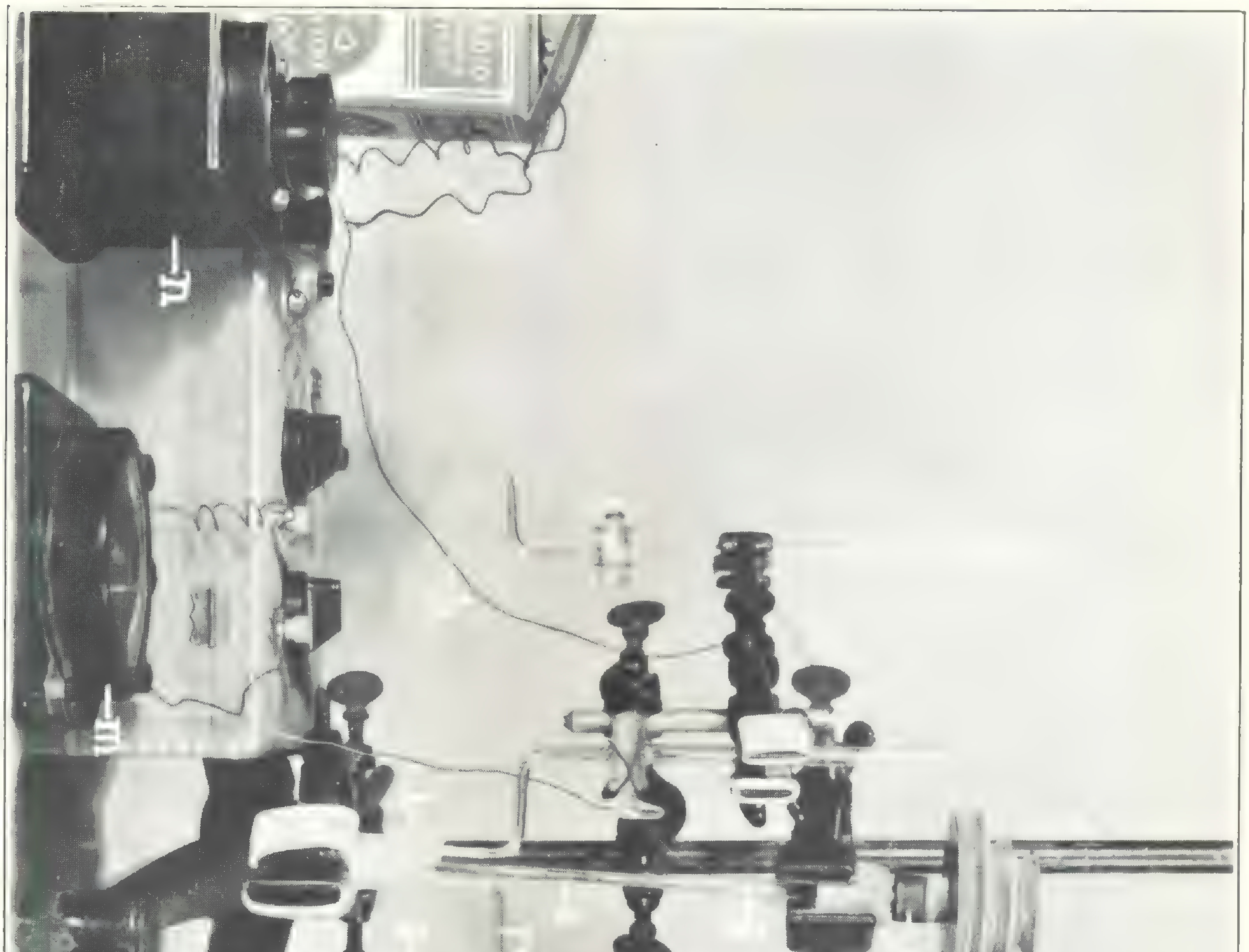
2

DAVIS—INFECTIOUS CHLOROSIS

Explanation of Plate

PLATE 10

Electrometric titration outfit which was used in the acidity experiments: *a*, glass tubing used for making connection with the platinum electrode, used also as a shaft for the stirring device; *b*, vial holding the sample to be titrated against standard alkali; *c*, salt bridge containing saturated KCl solution; *d*, burette, 2 cc. capacity; *e*, vessel containing a saturated calomel reference electrode; *f*, vial containing saturated KCl solution; *g*, wire leading from voltmeter to calomel electrode; *h*, wire leading from galvometer to quinhydrone-platinum electrode system; *i*, electric motor; *k*, sleeve of glass tubing for bearing; *l*, metal washer; *m*, millivoltmeter; *n*, galvanometer.



DAVIS—INFECTIOUS CHLOROSIS

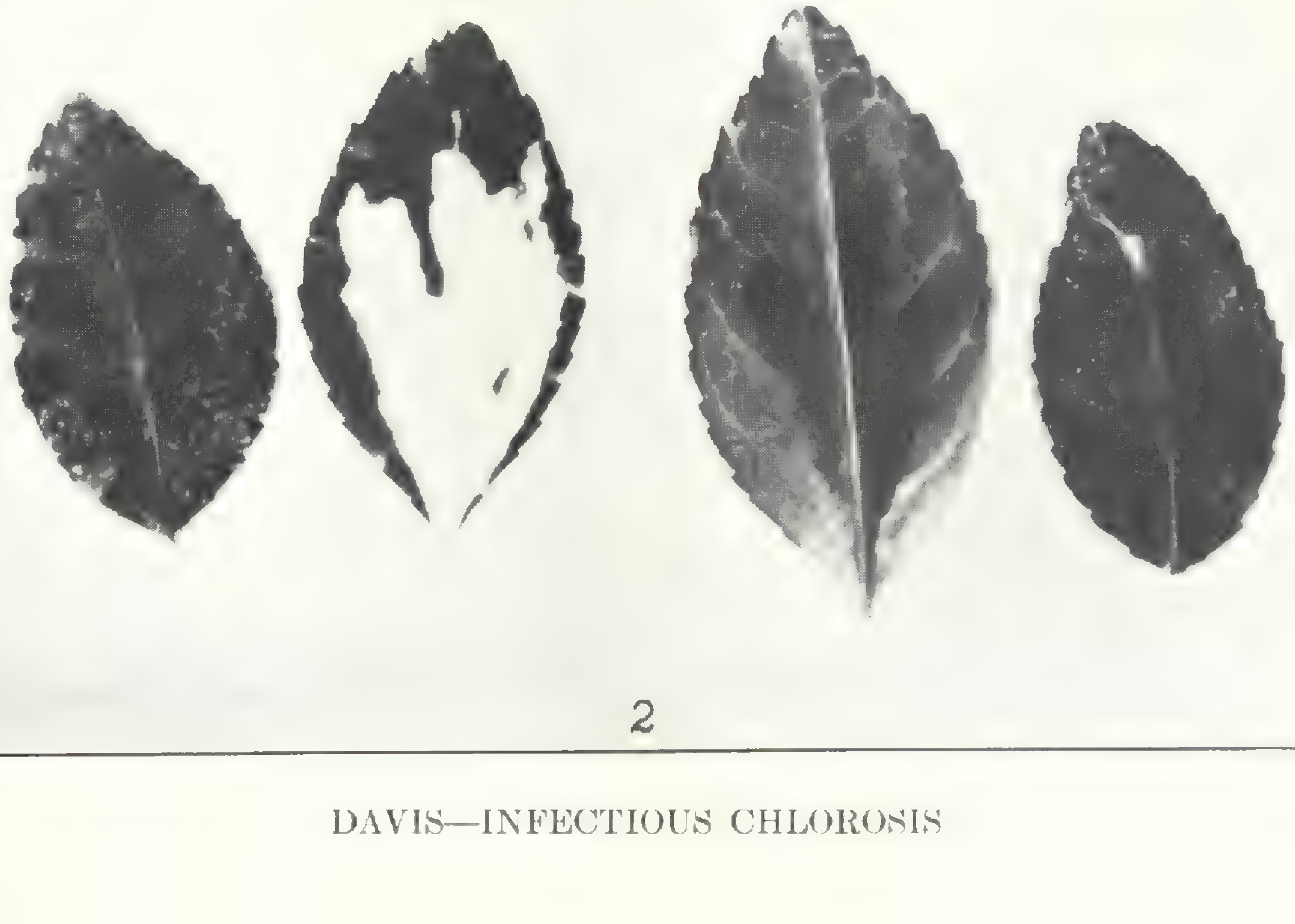
Explanation of Plate

PLATE 11

Fig. 1. *Abutilon Thompsonii*, showing effect of removing successive crops of variegated leaves: 1, variegated leaves permitted to remain attached; 2, all variegated leaves removed as they developed. Notice that the smooth, deep green leaves of this plant are all free from chlorosis.

Fig. 2. Detached leaves of *Evonymus japonica* vars. "*aurea*," "*medio-picta*," and a green variety showing infection of the green: 1, Showing infection with chlorosis resulting from graft with "*aurea*." Notice very inconspicuous mottling of the leaves; 2, Variety *medio-picta*, a type of non-infectious variegation; 3, Showing leaf of "*aurea*" variety which transmitted a chlorosis to the green; 4, Showing infection resulting from a bud of "*aurea*" which was inserted into the bark of the green individual.

1



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DAVIS—INFECTIOUS CHLOROSIS

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A MONOGRAPH OF THE HELICOSPOROUS FUNGI IMPERFECTI

DAVID H. LINDER

Mycologist to the Missouri Botanical Garden
Assistant Professor in the Henry Shaw School of Botany of Washington University

The group of Fungi Imperfecti characterized by helical spores, a group for the most part consisting of saprophytes which obtain their nourishment from decaying bark or wood, but also comprising a few members which are parasitic on phanerogams has been known for over a hundred years, the first species having been described by Link[1] in 1809.

The pioneers in the study of this group of fungi were chiefly concerned in describing numerous new species and establishing a number of genera to accommodate them. With the lack of adequate descriptions and delimitations of these, however, the increase in number resulted in confusion, to alleviate which various artificial classifications were proposed. Saccardo's system of classification is perhaps the most outstanding and most used. It was a step in advance but failed in some respects. To name an important source of confusion, one has only to consider two of the families of the Hyphomycetales, the Mucedinaceae and the Dematiaceae, which are separated, primarily, on the color of the spores and conidiophores. There are several helicosporous species which are transitional between these two families. In the genus *Helicoon*, for example, *Helicoon Richonis* is characterized by having fuscous spores and very short conidiophores, *H. auratum* by fuscous conidiophores and golden-yellow spores, *H. fuscosporum* by hyaline conidiophores and fuscous spores which are nearly hyaline when immature, and *H. farinosum* and *H. sessile* by entirely hyaline

[1] Link, H. F. Observationes in ordines plantarum naturales. Ges. Naturforsch. Freunde z. Berlin Mag. 3: 21. *pl. 1, fig. 35.* 1809.

conidiophores and conidia. All of these species, however, would be placed either in the Dematiaceae or Mucedinaceae, according to the Saccardan system. The system is not entirely to blame for the multiplication of names. The authors of the species should also be taken to task, since many of the early descriptions are so brief that it is next to impossible for the taxonomist to obtain anything but the haziest idea of a number of species, not only in this group but also in other groups of the Imperfecti. Often there are subtle distinctions in form that cannot be depicted except by drawings of the conidiophores or spores, yet frequently one or the other, or both, are omitted. Hence more doubt and more superfluous names add to the confusion which could be avoided easily by insisting that accurate illustrations should accompany the original description in order to validate the name of any microscopic fungus.

The aim of this paper, therefore, is to arrange the species in an orderly sequence with ample descriptions and illustrations, to relate where possible the sexual and asexual stages in the life history of the organisms, and to supplement these phases of the work with a comparative study of certain species in their development and biological reactions in culture by modern methods. For this reason the paper is divided into two parts,—the first part to deal with the study of the fungi in culture, the second to cover the taxonomy of the group.

Historical

The earlier workers in this group, aside from describing new species, covered to some extent the connection between the conidial forms and their perfect stages and a study of the course of development of the former. Handicapped as they were by their scanty facilities, the first writers made no efforts to obtain pure cultures. Hence there arose faulty ideas as to the nature of the helical conidia. Corda,[1] describing *Helicomyces aureus* as a new species, declared that the helical spores were parasitic on the sterile hairs of *Sphaeria exilis*, and three years later[2] he found them on what he thought were the sterile conidiophores of *Doratomyces olivaceus*. It seems much more probable, however, that these ster-

[1] Corda, A. C. I. Icones fungorum 1: 9, 15. 1837.
[2] Corda, A. C. I. Flore illust. Mucéd. d'Europe, pp. 29–30. 1840.

ile hairs of *Sphaeria* and of *Doratomyces* are in reality the conidiophores of *Helicomyces aureus*. Hence he unknowingly was the first to indicate connections between the imperfect stage, *Helicomyces*, and a perithecial condition. This was followed by further work on possible relations between the perfect and imperfect stages. Constantin,[1] in 1888, reviewing the genus *Helicosporium*, previously established by Nees von Esenbeck,[2] asserted that these forms were the conidial stages of *Crucibulum* and *Cyathus*, but gave no evidence to support his beliefs, which, in view of all subsequent work, appear to be without basis. The only instance that might possibly be interpreted as evidence for connections between the helicosporous forms and the Basidiomycetes is the occurrence of very small helical sporidia observed by Brefeld[3] to be produced on the germination of the basidiospores of certain species of *Exidia* and *Auricularia*, but they, in our modern conception of the nature of these spores, cannot be considered as homologous with the helical spores of the Fungi Imperfecti. Perhaps the first definite statement of connections between the Helicosporeae and a perfect stage was made by Plowright and Phillips[4] when they described *Sphaeria helicoma*, the conidia of which they state were similar to those of *Helicoma*, and emphasized by their choice of the specific name their belief in the interrelationship of the two forms. Cooke[5] expressed his doubt of this relationship, since he had also found in connection with the Sphaeriae other imperfect stages, such as *Helminthosporium* and *Monotospora*. Saccardo,[6] at a later date, accepted Plowright's idea and published not only his species but also Cooke's species of *Sphaeria* under the new names of *Lasiosphaeria helicoma* (P. & P.) Sacc. and *Chaetosphaeria parvicapsa* (Cke.) Sacc. and as such these were published and illustrated by Berlese.[7] More recently, in 1905, von

[1] Constantin, J. Les mucédinées simples. p. 101. 1888.

[2] Nees von Esenbeck, T. F. L. Das System der Pilze und Schwämme. p. 63. 1817.

[3] Brefeld, O. Untersuchungen aus dem Gesammtgebiete der Mykologie **7**: 69–94. 1888.

[4] Plowright, C. B. & F. L. S. Phillips. New or rare British fungi. Grevillea **6**: 26. 1878.

[5] Cooke, M. C. On black moulds. Quekett Microsc. Soc. Jour. **4**: 246–273. 1877.

[6] Saccardo, P. A. Sylloge fungorum **2**: 94, 192, 195. 1883.

[7] Berlese, A. N. Icones fungorum **1**: 27. *pl. 17.* 1890; 112. *pl. 113.* 1892.

Höhnel[1] published the new species *Helicosporium phragmites* which he says was "in Gesellschaft von *Acanthostigmella genuflexa* n. g. et sp., das vielleicht dazu gehört." This, one of the most recent statements indicating such relationships, is based on the mere occurrence of the imperfect and perfect stages together and emphasizes the necessity of establishing such relationships by exact studies in pure culture, for it would seem that by so doing a more natural line of division of the groups of the simple Sphaeriae might be arrived at, thus doing away with many of the unsatisfactory characters that are so often used in their identification.

The study of the imperfect forms in culture, on the whole, has been scanty. The first attempt at cultural studies was that of Zalewski,[2] who, in 1888, finding the unique spores of *Clathrosphaera spirifera,* carried on a series of experiments, not, however, in pure culture. During the course of these, as one of the accessory spore forms, he described a *Helicodendron* type of asexual spore, thus in the same year as Constantin announcing polymorphism in the Helicosporeae.

Four years later, Matruchot[3] made a study of the course of development of *Helicosporium lumbricoides* and reported as connected with the helical type, three additional spore forms,—a *Stemphylium,* a *Coniothecium,* and a "sclerote pedicelée." Of these the *Coniothecium* stage was the only one not shown by the drawing to be connected with the helical spores, but was, on the other hand, the only form that gave rise to them in culture. This stage, however, should not, it seems to the writer, be considered a separate form but rather a senile condition of the vegetative hyphae in which the cells have become swollen and colored, and deep constrictions have appeared at the septa,—a condition relatively common in cultures of this group. The *Stemphylium* type of spore, Matruchot states, was found but once, and then in a hanging-drop culture supplied with alkaline urine that was constantly renewed. It was said to be borne on the same hyphae as the helical spore, and was so illustrated; yet when it was transferred

[1] von Höhnel, F. Mycologische Fragmente. Ann. Myc. **3**: 338. 1905.

[2] Zalewski, A Przyczynki do zycioznawstwa grzybow. Rozpraw Spraw. Wydz. matem. przyr. Akad. Krakau **18**: 153–191. *7 pl* 1888.

[3] Matruchot, L. Recherches sur le développement de quelques Mucédinées, pp. 5–37. *pl. 1–8.* 1892.

back to normal environmental conditions it failed to give rise to the coiled conidia of *Helicosporium* and instead continued as a strain of *Stemphylium*. It seems to the writer, therefore, that although the "sclerote pedicelée" and the so-called *Coniothecium* are a part of the polymorphic life history of the asexual stage, the *Stemphylium* was a contamination that entered the culture during the renewal of the medium.

Investigations in which pure single-spore cultures were employed are those of Rand,[1] who in studying in detail the pathology and life history of *Helicosporium nymphearum* Rand, found that sclerotial bodies were produced, but from these, by none of the methods employed, was he able to obtain the perfect stage. This species, because of its parasitism on phanerogams and more especially because of the toruloid nature of its spores, should be placed in the genus *Gyroceras*, a combination made in the second part of this paper. More recently, Killian,[2] during the course of his investigations of the life history of *Gyroceras Celtidis*, has found in connection therewith a pycnidial, a sclerotial, and a perithecial stage, the last having previously been described as *Sphaerella Celtidis* Passerini. Of the sclerotial stage, Killian concludes that, although the exact nature is unknown, it appears to be an abortive perithecium. Such may be the explanation of the sclerotia found in culture by Rand.

From this brief survey, it is obvious that our knowledge of the group of helicosporous Fungi Imperfecti is in many respects meager. Is it evident also that there is need especially of comparative studies of representative species in pure culture to serve as a sound basis for classification, to extend our knowledge of the life history and biology of the group, and also where possible to correlate the perfect and imperfect stages.

Acknowledgments

This paper was begun while the writer was a graduate student in the Laboratory of Cryptogamic Botany at Harvard University, and was completed at the Missouri Botanical Garden. The

[1] Rand, F. V. Leafspot-rot of pond lilies caused by *Helicosporium nymphearum*. Jour. Agr. Res. **8**: 219–232. *pl. 69–70*. 1921.

[2] Killian, C. Le Gyroceras Celtidis Mont. et Ces. parasite du Celtis australis L. Soc. d'Hist. nat. Afrique Nord, Bull. **60**: 274–281. 1925.

experimental studies, appearing here in a condensed form, and the taxonomy of those species used were submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University. In addition to this, almost all of the bibliographical and much of the taxonomic work was accomplished at the Farlow Herbarium of the same institution.

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Part I. Studies of the Fungi in Culture

MATERIALS AND METHODS

These studies were made with pure cultures isolated from collections made by the writer in Canton and Cambridge, Massachusetts, and supplemented to some extent by comparisons with dried material in the writer's collection, in the von Höhnel herbarium, and in the herbarium of Dr. Thaxter.

Because of their inconspicuousness in some cases, and their none too frequent occurrence in others, these organisms proved rather difficult to gather together for a comparative study. After some field work, however, it became possible to recognize likely habitats, which are, for the most part, the moist under-side of the bark of limbs of deciduous trees that have fallen to the ground in shaded glens, at the borders of brooks or swamps, or in moist fields,—in general, wherever there is a fair degree of moisture the year round. Bark is most suitable for the growth of the fungi when it is somewhat weathered, and when it has just separated from fallen logs it is especially likely to bear the organisms in question. Wood also frequently serves as a substratum, chiefly when it is moist and just beginning to soften with decay.

Isolation of the fungi of this group gave considerable trouble at first. Because of the size of the spores, the somewhat gelatinous sheath that they secrete, and the presence of other fungi among or near the colonies, there is an abundance of foreign spores that cling to the ones desired and make the simpler methods of isolation of doubtful, or at least uncertain, value. Of the methods tried, the poured-plate method of the bacteriologist proved of little value in the present researches; the Barber spore picker, although used to a limited extent, was tedious, and when the spores were isolated not only were they often contaminated with bacteria but in some species a large percentage failed to germinate. The other method employed while in the field was simple though prolonged. The spores were picked off, under a hand lens, with a sterile platinum needle and transferred to an acid medium where they were allowed to germinate. As the hyphae from the germinating spores grew clear of the bacterial colony they were transferred to a more favorable medium. Undoubtedly the best procedure was Wehmeyer's[1] modification of the sprayed-spore method used by Kauffman. The spores were transferred to 10 cc. of sterile water, 2 or 3 drops of 10 per cent lactic acid added, and then after a thorough shaking to distribute the spores a quantity of the solution was taken up in a sterile pipette and sprayed on an agar plate which was then tilted back and forth until there was an even

[1] Wehmeyer, L. E. The imperfect stage of some higher Pyrenomycetes obtained in culture. Mich. Acad. Sci. Arts & Letters, Papers 3: 245–266. 1923.

distribution. The spores were cut out singly under the microscope as they began to germinate. This treatment not only washed out the larger contaminating spores from the helical ones, but the addition of acid also inhibited the growth of bacteria.

Various agars, such as corn-meal infusion, carrot, chestnut bark, and potato-dextrose agars, were used for general culture work. While they were all satisfactory for this, chestnut-bark infusion agar, made by allowing 250 grams of the bark to stand a week in a litre of water, straining off the liquid and then adding 4 per cent of agar, made a favorable acid medium for isolation, and was almost exclusively used for that purpose. Potato-dextrose agar was an easily available and readily prepared medium that was of value for cultural work and, because of its transparency, was utilized when van Tieghem cells were employed. In addition to these, Pethybridge's rolled-oat agar, as used by Wehmeyer, was found to be an exceedingly good substratum for studying the natural behavior of the fungi on artificial media. In fact, this is the only one on which nearly all species showed normal color and conidium production. For hydrogen-ion work, Pfeffer's solution, as prepared by Gillespie,[1] with the addition of 4 per cent agar, was used; the solution being made acid by citric acid, and basic by NaOH. The solutions were tested by the colorimetric method before and after sterilization. To insure uniformity of material, a large amount of medium was made up at one time. A similar procedure was followed when Schmitz's[2] solution with 4 per cent agar was prepared and tests made with maltose, xylose, wheat starch, pectin, cellulose, and asparagin. The pectin was prepared by the method advocated by Baxter,[3] and the cellulose by that worked out by Northrup.[4] In this connection it should be emphasized that the $FeCl_3$ used as a solvent for cotton should be maintained at a temperature just high enough to keep it molten; should this be

[1] Gillespie, L. J. The growth of potato scab organism at various hydrogen-ion concentrations as related to the comparative freedom of acid soils from the potato scab. Phytopath. 8:257–269. 1918.

[2] Schmitz, H. Relation of bacteria to cellulose fermentation induced by fungi with special reference to the decay of wood. Mo. Bot. Gard. Ann. 6: 93–136. 1919.

[3] Baxter, D. V. The biology and pathology of some hardwood rotting fungi. Am. Jour. Bot. 12: 522–554. 1925.

[4] Northrup, Zae. A new method of preparing cellulose for cellulose agar. Abstr. Bact. 3: 7. 1919.

exceeded and the solution boil, the resulting precipitate will be charred.

Observations occasionally were made from material growing in test-tubes or in 250-cc. Pyrex flasks. Especially was this done when experiments were to run for a considerable length of time, but van Tieghem cells and Petri dishes proved most convenient,—the former when the earlier stages of the development of the fungus or the germination of spores was being examined, the latter when experiments in which the growth of a colony was to be measured, as in the study of the effect of hydrogen-ion concentration, temperature, and of different organic substances. In such cases, measurements were made radially from the edge of the inoculum to the periphery of the colony. The cultures were allowed to grow a week or more before the first measurements were taken. After this they were again allowed to grow for a varying length of time, at the end of which a second series of measurements was made. The rate of growth was then determined by dividing the difference in the amount of radial growth by the number of days elapsed. By following this procedure, the effects of nutrient material on the fungus mycelium and also on the substratum transferred therewith were avoided, and the availability of the carbohydrates in the media to be tested was more definitely shown.

LIFE HISTORIES

The group of helicosporous Fungi Imperfecti is one including 11 genera and comprising over 75 species. Of these, only the species included in the Dematiaceae and Mucedinaceae will be considered here. Of the 7 genera of the above-mentioned families, representatives of 5 have been cultured and compared as to their life history and relations to environment. These are *Helicoma Mülleri*, *H. Curtisii*, *Helicosporium aureum*, *H. gracile*, *Helicomyces scandens*, *Helicodendron tubulosum*, *H. triglitziensis*, and *Helicoon sessile*.

The life histories of the representatives studied in this part of the paper were most conveniently worked out by following their growth in van Tieghem cells, supplemented by observation from tube cultures and from freshly collected material.

Germination of spores takes place readily either in water or on

a nutrient substratum. The one requirement, as will be seen later, is that the relative humidity be sufficiently high. At first there is an increase in the turgor of the spore, resulting shortly in the rupture of a sheath or exospore (pl. 14, fig. 7; pl. 30, figs. 1–2). This exospore, although not previously reported so far as the writer is aware, has been observed to crack off in all species studied except *Helicoon sessile*, *Helicodendron tubulosum*, and *H. triglitziensis*. Often, although it is hyaline, it is quite pronounced, even on the ungerminated spores. In the case of *Helicosporium aureum* and *H. gracile*, when the exospores are cracked off, it is found that they are permeated with a yellow color characteristic of the spores of that species, and that the spore proper is hyaline.

Following the rupture of the exospore, germination tubes are produced. The spores of *Helicoma Mülleri*, *H. Curtisii*, and *Helicosporium gracile* typically begin to germinate merely by the elongation of their terminal cells, following which they arise from any of the central cells. With the remaining species, one or more of the central cells almost invariably germinate first, while the end cells remain inactive and at times fail to swell, thus appearing as dwarfed appendages to the neighboring inner cells. Although all the cells of a given spore are capable of germinating, it has never been observed by the writer that they do so, even though they may undergo swelling. Just what the function of these inactive cells may be cannot be stated definitely, yet there is a suggestion that they may serve as a reserve of nourishment for the more vigorous and more rapidly germinating ones.

Once the germ tube is formed, growth proceeds rapidly in most species, and shortly the hyphae begin to branch and anastomose. Later the hyphae of all species but *Helicodendron triglitziensis* and *Helicoon sessile* become some shade of brown. At first only one or two cells are colored but soon all the older parts of the colony become involved. At or just previous to the production of the pigment, the cells in or near the center of the colony swell between the septa, and a pseudoparenchymatous mat of swollen cells results, resembling that already described for *Helicodesmus*.[1]

[1] Linder, D. H. Observations on the life history of Helicodesmus. Am. Jour. Bot. **12**: 259–269. 1925.

Helicosporium aureum, however, does not produce such a mat. Instead, several adjacent cells swell up, divide in various directions (pl. 14, figs. 5–6), and form a compact, darkened mass of cells that resemble perithecium initials. These later result in rounded perithecium-like bodies which on examination prove to be soft and sterile, remaining in that condition even after three months. It is quite possible that these bodies may represent the immature stages of the "Sphaeriae exilis" mentioned by Corda.

Helicoon sessile shows an interesting modification of the pseudoparenchymatous mat, if it can be so termed. The hyphae do not swell as did those of the other species. Instead, there is a tendency for the hyphae to grow parallel and close together to form flat strands, between the elements of which there are frequent fusions by means of lateral processes (pl. 26, fig. 15). Such strands, although having their origin in the center of the colony and in the deeper layers, are much more elaborate near the surface of the substratum, natural or artificial, or under conditions such as exist on the sides of the test-tubes above the agar where the available concentration of nourishment and moisture is relatively low. Under such circumstances, these strands apparently serve the purpose of transporting food material and of retaining moisture. Frequently, when single hyphae have become dry and have lost their turgidity, a liquid substance has been observed between the turgid elements of the strands.

When the conidiophores form, they may do so in two general fashions: They may arise merely as branches of surface or aerial mycelium from which they are distinguished with difficulty, or they may arise as somewhat differentiated and specialized branches of the mycelium in the substratum. The first type is characteristic of all but four of the species studied here. Upon this type of conidiophore the conidia are borne singly on teeth that are generally pleurogenous on the upper surface of the repent mycelium, but frequently they are acrogenous on short, erect, little-differentiated branches. The second type of conidiophore is characteristic of *Helicosporium aureum*, *H. gracile*, *Helicoma Curtisii*, and *H. Mülleri*. The differentiation is evident from the beginning. Two, three, or more adjacent cells of the creeping sterile hyphae swell, become colored, and send out erect branches that are concolorous

with the fuscous or subfuscous swollen cells of the vegetative hyphae. This branch, after elongation, is quite definitely a conidiophore, not merely a side branch of the repent or aerial mycelium. Such conidiophores after repeated spore formation may then commence to branch in a manner characteristic of the species.

Spore formation next takes place. A bud begins to form on the terminal cell of the conidiophore, or on the side if the species bears the spores pleurogenously. This bud or bulge elongates and shortly swells to the diameter of the mature filament, leaving a constriction at the base that becomes the tooth or sterigma. After reaching somewhat less than half the diameter of the eventual spore, the filament curves over and grows in two planes, or three planes in the case of *Helicoon* and *Helicodendron.* In *Helicosporium aureum* especially, and in other members of *Helicosporium* not considered in this part of the paper, the teeth show an interesting behavior. When first formed they are slender and cylindrical, but later, at the point of attachment to the conidiophore there is a swelling which develops into the hyaline bladder-like lateral projection on which more teeth are produced and more spores formed. In even older portions of the sporogenous area of the conidiophores, these projections may become so elongate, even slightly colored, as to have the appearance of a short lateral branch. Frequently in those species which produce their spores pleurogenously, many of the spores may be acrogenous at first. In *Helicoma Mülleri,* for example, the first spore is formed at the apex of the terminal cell. With the elongation of the terminal cell, a process that continues as the conidium reaches maturity, the first-formed conidium is pushed to one side and another spore is produced on the new apex of the conidiophore. When a single spore, or not rarely three or four spores, have been produced in this fashion on the terminal cell, a cross-wall is laid down above these spores, now lateral, and the process continues. Lateral conidia may also be produced on new or previously occupied sterigma of the lower cells, but when they are produced on previously occupied sterigma, those sterigma are usually branched (pl. 21, fig. 15).

Cultural studies with the species used in these experiments gave little evidence of polymorphism, although further evidence was constantly sought. The writer, using *Helicodendron tubulosum,*

the same species, so far as can be determined, studied by Zalewski, failed to find the long list of forms which that author published. Zalewski's experiments were repeated three or four times without success. While cultural experiments failed to strengthen the evidence for polymorphism in the species mentioned, in nature, very rarely, another type of spore is produced by *Helicosporium aureum*. It is quite different from the helical spore, being brownish and ovoid (pl. 14, fig. 3) and produced on the slightly colored tip of the conidiophore in the early stages of development. It is with hesitation that this form of spore is reported, since it has been found only once by the writer, although its occurrence was indicated more frequently by the blunt teeth, pleurogenously borne, just below the apex of the conidiophore. It may have been these spores that suggested to Corda that the helical spores were parasitic on *Doratomyces*. The "sclerote pedicelée" of Matruchot has been observed in herbarium material of *Helicosporium nematosporum* and *Helicoma proliferum* and is undoubtedly a part of the life history of these species.

RELATION BETWEEN PERITHECIAL AND CONIDIAL STAGES

During the course of these experiments, many methods were tried in the hope of producing the perfect or perithecial stage of these fungi: They were grown on different media, under different conditions of temperature and humidity, and strains from different localities and different natural substrata were contrasted, but these attempts were fruitless. However, in the course of collecting the different conidial forms, the writer was fortunate enough to find the perithecia of *Lasiosphaeria pezizula* growing in connection with *Helicoma Curtisii*. Single-spore cultures were made by Wehmeyer's method, as previously described, and the life history was followed in pure, single-spore culture, from the ascosporic to the conidial stage. The ascospores (pl. 21, figs. 3–5) whether hyaline, or deeply colored as they are at maturity, when transferred to a suitable moist medium, germinate after two or four days, or somewhat more slowly than the conidia. The two end cells invariably germinate first (pl. 21, fig. 6) and then are followed by the central cells, some of which may not send out hyphae. At the end of two weeks at laboratory temperature, the mycelium gave rise to the

conidia of *Helicoma Curtisii*, thus establishing the connections between the two forms. Although single-spore and single-ascus cultures have been maintained for five months on various media, as yet no perithecia have been produced. It is hoped, however, that further experimental work may yet make it possible to complete the cycle.

RELATION TO ENVIRONMENT

GROWTH ON ARTIFICIAL MEDIA

Helicoma Mülleri Cda. — *Helicoma Mülleri*, at best not a rapidly growing form, produces mycelium and spores very slowly on chestnut and carrot agars. It does, however, grow rather rapidly on potato-dextrose agar and rolled-oat agar, both of which support a vegetative growth similar to that found in nature. In respect to its nearly normal growth on potato agar, this fungus is unique among those studied,—the other species producing on this medium an abundance of aerial mycelium at the expense of spores.

When grown on Schmitz's solution agar to which maltose, wheat starch, xylose, pectin, cellulose, or asparagin have been added, growth, as is shown in table I, is most rapid on xylose, followed in order by pectin, maltose, wheat starch, and cellulose, with very little or none on asparagin. The color of the colonies on

TABLE I

Medium	Av. growth in mm. after		Rate of growth per day	Relative per cent of sporulation
	12 days	20 days		
Maltose	1.8	4.1	.29	60
Wheat starch	1.0	4.3	.24	30
Pectin	2.0	5.3	.44	100
Xylose	1.8	5.5	.46	80
Cellulose	.37	2.8	.18	—
Asparagin	.00	.00	.00	—

these media also varied to some extent: on xylose, pectin, and starch, they were "Buckthorn Brown";[1] on maltose, "Cinnamon Brown"; and on cellulose they were nearly hyaline. There was also a pronounced "Mars Brown" discoloration in the medium when xylose and pectin were employed; wheat starch agar was

[1] Ridgway, R. Color standards and nomenclature. Washington, D. C., 1912, used where colors are in quotation marks.

less discolored, and the color present was confined to the immediate vicinity of the buried hyphae, while on maltose there was very little discoloration. Spore production was best on pectin and xylose, as is shown by the above table, and appears to be correlated to an extent with the coloration of the hyphae and the amount of discoloration in the agar. From the evidence presented, it appears that materials of the nature of pectin and xylose are important as sources of food material for the fungus, and that on the availability of these depends the ability of the fungus to dissolve cellulose and thus to penetrate the substratum of bark upon which the species is most frequently found.

Helicoma Curtisii Berk.—With the various organic materials used to test the availability of substances that might occur in the natural substrata, it was found (table II) that *Helicoma Curtisii* made the greatest growth on maltose, followed closely by xylose and pectin, and to a lesser degree by wheat starch, and cellulose.

TABLE II

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	12 days	20 days		
Maltose	1.2	4.1	.36	—
Wheat starch	1.0	2.0	.12	—
Pectin	1.8	4.0	.27	50
Xylose	1.8	4.1	.29	100
Cellulose	.5	.5	.00	—
Asparagin	.41	.41	.00	—

On maltose, which vied with xylose and pectin as being the most favorable agar medium for vegetative growth, there was no sporulation, yet on the last two this did occur. On the media which were apparently most favorable for vegetative growth, the mycelium, unless masked by the presence of brownish conidiophores, was yellowish in color, a character manifested on all artificial substrata and apparently characteristic of this species in culture. It is interesting to note that, although this species grows more frequently on wood, cellulose is less available as a source of nourishment than it is for *H. Mülleri*. This may perhaps be explained by the fact that when the fungus does occur on wood, the hyphae are chiefly to be found in the wood rays, and it is possible that enough avail-

able carbohydrate material is still present to support growth. This seems quite plausible, especially since in those cases in which the writer has found it on wood, the hyphae have followed closely the zone vacated by the bark as it separated from the wood, where the soluble carbohydrates are less likely to have dissolved away.

Helicosporium aureum (Cda.) Linder.—Since this species grows chiefly on old coniferous boards, very rarely on bark, it is of interest to note its relation to the substratum. Longitudinal sections of a pine board, on which the fungus was growing luxuriantly in nature, show that the hyphae do not follow along the wood rays as do those of *Helicoma Curtisii*, but instead pass from cell to cell, irrespective of the nature of the tissues, either by way of the bordered pits or else by direct penetration of the cell walls. The hyphae are 2–5.5 μ in diameter, brownish in color, becoming sharply constricted where they pass through the cell walls, and give rise laterally to delicate hyaline or slightly colored branches (pl. 14, fig. 8) 1.8 μ in diameter, that grow closely applied to the inner surface of the cell wall. These delicate branches grow closely applied to the inner surfaces of the cell walls and penetrate the pits at frequent intervals.

To determine approximately what food substances this fungus requires it was grown on the media already used for the two species of *Helicoma*. The results, embodied in table III, show that

TABLE III

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of perithecial bodies
	14 days	20 days		
Maltose	2.1	3.1	.16	00
Wheat starch	2.0	2.8	.13	100
Pectin	3.6	5.3	.27	50
Xylose	.45	.58	.02	00
Cellulose	1.9	2.6	.12	30
Asparagin	.37	.44	.01	00

pectin was the most favorable carbohydrate for vegetative growth, followed in the order named, by maltose, wheat starch, and cellulose. Spore production, however, took place only on pectin and maltose. The production of the perithecia-like bodies, mentioned in the consideration of the life histories, was greatest on the wheat-

starch medium, less on pectin and cellulose. On the remaining media no such bodies were produced. From this evidence and from the penetration of the hyphae into the bordered pits, it seems safe to conclude that pectin or pectin-like material plays an important rôle in the vegetative growth and spore production of this fungus.

A comparison of the development of the conidiophores and spores on artificial media with that on the natural-wood substratum shows that only on oatmeal agar do growth and reproduction take place as on the natural wood. On none of the other agars is spore production or the color or nature of the mycelium the same as in nature. For example, the conidiophores on potato-dextrose agar, instead of being stiff, erect, and seta-like, tend to grow very rapidly and to become a tangled mass of semi-repent or arched hyphae, for the most part bearing the spores in the typical fashion on bladder-like lateral projections (pl. 14, figs. 1, 5), but also producing some on the apex of the hyaline branches. Because of the fact that the spores under such conditions are produced terminally on branches, there may arise some doubt as to the value of the bladder-like projections as taxonomic characters. However, it is rather of interest as throwing light on the probable origin of these projections,—namely, from the suppression and specialization of the branches for the purpose of bearing spores. This hypothesis is further supported by the fact that after the first spores are produced, the projections lengthen, bear more spores, and occasionally, even on natural substrata, continue growth, becoming rather deeply colored and acquiring the nature of branches. The color of the colonies on potato-dextrose agar, as on most of the synthetic media, is "Citrine Drab" and is scarcely altered by the presence of the feebly colored spores; in nature and when cultivated on rolled-oat agar, it varies from "Wax Yellow" to "Dull Citrine Drab," depending on the number of spores present. Under such conditions also, the conidiophores are seta-like and deep fuscous.

Helicosporium gracile (Morgan) Linder.—Although growing well on most media tried, only on rolled-oat agar did *Helicosporium gracile* produce mycelium and spores resembling those of the natural growth on moist decaying bark. As is shown in table IV,

TABLE IV

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	9 days	12 days		
Maltose	3.0	4.5	.50	00
Wheat starch	2.5	3.8	.43	50
Pectin	4.6	5.6	.33	100
Xylose	3.3	4.1	.27	00
Cellulose	2.1	4.1	.66	20
Asparagin	2.3	2.6	.10	00

growth on the various carbohydrate media, if the size of the colony be regarded as a criterion, is greatest on pectin, as is the relative percentage of sporulation. The color of the colonies on maltose and xylose was "Russet," the former with a "tawny" peripheral zone, the latter with a yellowish one; on wheat starch they were "Cinnamon Brown" with little aerial growth; on pectin "Mummy Brown" but covered by a weft of grayish hyphae; and on cellulose they were "Buckthorn Brown" with aerial hyphae relatively sparse. Spore production occurred continually on pectin, wheat starch, and cellulose, as shown in the table above. On maltose, however, there was only a slight amount of sporulation, and that only for a short period.

Helicomyces scandens Morgan.—On the natural bark substratum, colonies of *Helicomyces scandens* appear to be confined to the inner layer, that is, to the tissues nearest the cambium layer. In these tissues, however, there appears to be no apparent selection of the elements, and the hyphae penetrate in all directions while obtaining available nourishment.

The nature of this nourishment, shown by the following experiment and summarized in table v, varies considerably from that

TABLE V

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	12 days	20 days		
Maltose	3.0	6.0	.262	00
Wheat starch	2.4	6.3	.49	40
Pectin	1.8	5.8	.50	30
Xylose	1.6	5.6	.50	00
Cellulose	3.1	8.5	.66	100
Asparagin	.83	4.0	.39	00

required by the majority of the other members of the group studied in this portion of the paper, in that cellulose is by far the most important source of carbohydrate material. The production of spores, also, is greatest on cellulose agar, much less on wheat starch and pectin agars, and none at all on maltose, xylose, and asparagin agars. On all the media except asparagin agar, the mycelium at the surface of, or in, the substrata, was colored some shade of brown: on maltose and wheat starch "Sepia"; on pectin and xylose, "Isabella Color"; on cellulose, "Dark Olive Gray," but on asparagin it was very dilute "Olive Gray." It can thus be seen that the nature of the substratum, in this species at least, has a marked influence on the color of the vegetative growth.

This species grows well and produces conidia on most artificial media, but here again rolled-oat agar proved most favorable. In spite of the fact that spores were produced in abundance, the setae formed under natural conditions on the bark substratum were not produced, even though the cultures were grown under a variety of conditions. Only when grown on potato-dextrose agar in van Tieghem cells were the setae in evidence, and then only in a very rudimentary stage beyond which they did not develop (pl. 12, fig. 3). Morgan[1] says of these setae, "I have not been able to convince myself that the black pointed threads which they (the hyaline conidiophores) usually enclose are not the erect stem of some black mould." From observations of many cultures the writer at first entertained these same doubts, and in an attempt to solve the question grew this with other wood-inhabiting Fungi Imperfecti that produced erect fertile hyphae, but the conidiophores of *H. scandens* did not climb these in any case. Whatever doubt that remained was removed later as a result of the careful study of an abundance of freshly collected material. In this, it was quite evident that the setae were produced as the colonies aged, and generally where the conidiophores, usually repent, had become ascending and fasciculate. The setae may easily be traced downwards to the hyaline hyphae that bear them, and these, not infrequently, may be found to bear conidia.

[1] Morgan, A. P. North American Helicosporeae. Cinci. Soc. Nat. Hist. Jour. **15**: 39–52. 1892.

Helicodendron triglitziensis (Jaap) Linder.—The earlier studies[1] on the relation of the media to the growth of this species showed that, when observed in van Tieghem cells, lactose, fructose, glucose, and saccharose had no apparent influence on the abundance of the mycelium. When, however, in the present cultural studies, a comparison is made of the colonies of the fungus on maltose, wheat starch, pectin, xylose, and cellulose, the greatest amount of growth, as measured radially, is found on pectin agar, maltose, wheat starch, xylose, and cellulose following in the order named.

TABLE VI

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	9 days	12 days		
Maltose	16.8	28.3	3.81	00
Wheat starch	16.7	25.3	2.84	00
Pectin	19.6	29.6	3.31	00
Xylose	16.6	24.1	2.50	00
Asparagin	7.1	9.3	.72	00
Cellulose	13.8	18.8	1.61	00

If the rate of growth be compared, then maltose appears to be most favorable for growth, followed by pectin, the order of the other media remaining the same.

Helicodendron tubulosum (Reiss) Linder.—*Helicodendron tubulosum* was found growing with *Helicodendron triglitziensis* on well-decayed, very wet twigs of *Salix lucida*. While these two species superficially appear alike, they may readily be separated on morphological characters of the spores. In culture the differences between the two species are very marked. *H. triglitziensis* does not produce pigment or colored hyphae in the substratum, while *H. tubulosum* does; the mycelium of the former is superficial, appressed, and hyaline, of the latter, aerial, loose, cottony, and some shade of gray (pl. 30, fig. 4). On corn-meal decoction, corn-meal decoction agar, potato-dextrose agar, and on rolled-oat agar, *H. tubulosum* produces an abundance of aerial mycelium, and of hyphae which grow through the substratum, turning it brown or black. The aerial mycelium in the center of the colony is "Wood

[1] Linder, D. H. Observations on the life history of Helicodesmus. Am. Jour. Bot. 12: 259–269. 1925.

Brown," shading to "Puritan Gray" near the periphery, which is often dilute buff; the colony is generally indistinctly zonate.

When growth on the different carbohydrate materials and asparagin is compared it is found to be equally rapid, within limits, on all. However, as is shown by table VII, while radial growth is most rapid on pectin and cellulose, the aerial mycelium is produced

TABLE VII

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	9 days	12 days		
Maltose	8.1	15.3	2.24	80
Wheat starch	8.8	17.3	2.81	70
Pectin	11.3	21.6	3.42	60
Xylose	8.5	18.0	3.16	10
Cellulose	7.5	19.6	4.03	100
Asparagin	4.6	4.6	.00	00

rather sparsely. Spore production took place at the end of ten days, in relatively small quantities, on pectin. When, however, the cultures were exposed to freezing temperatures for two weeks and then brought back into the laboratory and maintained at room temperature, spores were produced readily on maltose, starch, and pectin, but especially abundantly on cellulose, in the proportions indicated by the table above. In respect to the color and nature of the mycelium, the fungus behaves most nearly as it does in nature when grown on pectin and cellulose. As has just been stated, on pectin and cellulose the mycelium was sparse, but on maltose, wheat starch, and xylose, dense pulvinate masses were formed. In nature, therefore, in all probability it is the cellulose and pectin of the decaying wood that is the source of carbohydrates for this species.

Helicoon sessile Morgan.—This species grows on very wet, decayed wood of deciduous trees, most commonly on maple and elm fallen at the edge of a brook or swamp or in similar wet localities.

Inasmuch as growth of the fungus is restricted in nature to such conditions, it is of interest to compare it on such substrata as asparagin and the various carbohydrates, and under different degrees of humidity, this last factor to be considered in a later chapter. Reference to the accompanying table shows that maltose and

TABLE VIII

Medium	Av. growth in mm., after		Rate of growth per day	Relative per cent of sporulation
	9 days	12 days		
Maltose	8.0	14.0	2.00	00
Wheat starch	6.8	7.6	.27	00
Pectin	10.0	14.6	1.53	00
Xylose	6.1	14.0	2.63	00
Cellulose	6.3	11.6	1.76	100
Aparagin	6.2	6.2	00	00

xylose are the most favorable for growth, yet only on cellulose, a mediocre source of nutrition, are spores produced. Such conditions as are exhibited by the cellulose medium appear to favor sporulation, since when the plant is grown on plain agar plus .3 per cent dextrose or saccharose, or even on very moist plain agar without sugar, spores are produced in relative abundance, generally in the zones where the mycelium is most dense. On potato-dextrose agar, however, spores are not produced, but instead there is an abundance of mycelium, thus bearing out an assumption that a less readily available supply of food material is conducive to spore formation. The development on rolled-oat agar is apparently inconsistent, since the spores are produced in relative abundance, accompanied by a luxuriance of growth. When the rolled oats were tested, however, it was found that the carbohydrates present consisted mostly of starch on which, as may be seen in the above table, vegetative growth takes place to but a slight degree. On analysis, tests for reducing sugars by Trommer's method gave negative results, thus showing that rolled-oat agar is similar to cellulose agar or other media in which the carbohydrate supply is not readily available. On the rolled-oat and the potato-dextrose agar substrata, the color of the mycelium is at first pure white, but with age becomes a beautiful shell-pink. Before pure cultures were obtained, it was noticeable that the presence of certain bacteria and yeasts induced still deeper coloration.

DISCUSSION

Color variations in the spores, conidiophores, and other aerial parts of the plant have been used for the purpose of distinguishing varieties, species, and even genera. As this basis has been used in

this group also, it is of interest to learn how variable that character may be and what factors are concerned in its variability. Of the many factors that might be involved, the most important, in the light of present researches, is the nature of the carbohydrate present in the substratum. Should carbohydrates be lacking, or should they not be available, as, for example, when *Helicoma Curtisii* is grown on asparagin or cellulose agars, the aerial mycelium, usually dark, is almost hyaline. With *Helicoon sessile,* the presence of certain bacteria or yeasts also may stimulate the production of color. Different degrees of hydrogen-ion concentration and of temperature, as will be observed later, may also cause color variations, but these factors are only of secondary importance as compared to the effects of the presence or absence of the different carbohydrates. Spore color appears within limits to be fairly constant, but may vary as to intensity. Formation by the mycelium of pigment and the diffusion of it into the substratum are also dependent on the nature of the medium. *Helicoma Mülleri* and *H. Curtisii* produce a soluble pigment on potato-dextrose agar, for example, while on Pfeffer's solution agar no pigment is produced.

As a result of these culture experiments with Schmitz's solution agar to which have been added the various carbohydrates and asparagin, it is difficult in all but one or two instances to see any correlation between vegetative growth and spore production. In certain cases, maximum sporulation accompanies maximum growth, as is exemplified by *Helicomyces scandens* and *Helicodendron tubulosum* when grown on cellulose agar, but here the correlation ceases, for second-best growth and second-best spore production apparently do not coincide. Each species has its peculiar requirement.

By a study of the accompanying chart (fig. 1) it will be seen for the majority of these saprophytic wood-inhabiting species, pectin, xylose, and cellulose, sugars similar to maltose, and even starch, make valuable sources of nutriment,—substances that are present in the natural substratum. Only *Helicoma Curtisii* shows no appreciable ability to utilize cellulose. Other carbohydrates are utilized in varying amounts, depending on the species. The utilization of these materials probably has little effect on the substratum unless the presence of certain sugars may allow a more

luxuriant growth and thus aid in the penetration of the wood by the fungi. Such a statement has been made by Rhoads[1] who says that xylose appeared to support the growth of *Collybia velutipes* and *Pleurotus ostreatus,* wound parasites of *Lupinus arboreus.* The species here considered, however, have never been found to be parasitic or wood-destroying in the economic sense of the word. Their rôle, judging by their slow growth and the nature of the carbohydrates utilized in culture, apparently is only to hasten the decay of wood and bark that has already begun to decompose. However, as Hubert[2] has already pointed out in the case of *Lasiosphaeria pezizula,* the ascigerous stage of *Helicoma Curtisii,* it is possible that some species may cause a certain amount of damage by their ability to discolor wood, or even to cause loss of strength in or near the parts infested by the mycelium. That the discoloration of the wood is not entirely due to the presence of fungus mycelium, as pointed out by that author, may be judged from the fact that *Helicoma Curtisii* produced on xylose agar a conspicuous "Mars Brown" discoloration. At all events, if ordinary precautions are taken in the storage of lumber, especially as regards ventilation, it seems that there is little likelihood of these fungi ever causing serious losses. Indeed, although this factor is dismissed by Schmitz[3] in the case of certain basidiomycetous wood-destroying fungi, it is quite probable that the typically saprophytic members of this group of helicosporous species may depend to a degree on the activity of cellulose bacteria.

SPORE PRODUCTION ON NATURAL SUBSTRATA

With the wide range of substrata on which some species grow, it is desirable from the taxonomic point of view to determine if any differences are created in the morphological characters of the spores, and to compare the material from the natural substrata with that from an artificial one. For this purpose, since they have larger spores and are more easily measured, *Helicoma*

[1] Rhoads, A. S. The pathology of Lupinus arboreus with especial reference to the decays caused by two wound parasites—Collybia velutipes and Pleurotus ostreatus. Phytopath. **11**: 389–404. 1921.

[2] Hubert, E. E. Notes on sap-stain fungi. Phytopath. **11**: 214–244. 1921.

[3] Schmitz, H. Relation of bacteria to cellulose fermentation induced by fungi with especial reference to the decay of wood. Mo. Bot. Gard. Ann. **6**: 93–136. 1919.

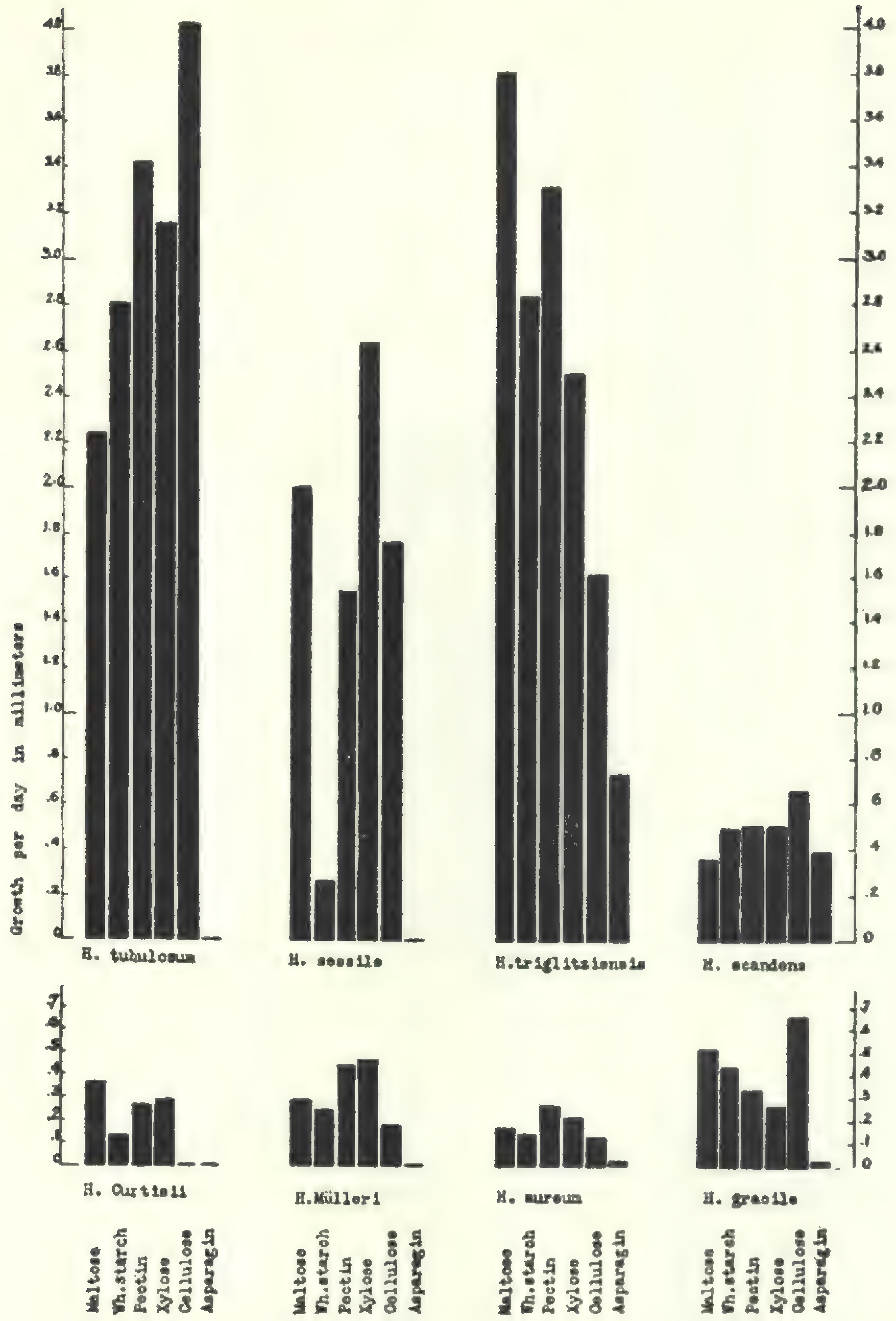


Fig. 1. Influence of substratum on rate of growth.

Mülleri and *H. Curtisii* were used. Accordingly, four sets of measurements were made for each of the two species growing on different hosts and on potato-dextrose agar. The spores were all mounted in 70 per cent alcohol; eosin-glycerine was allowed to run under the cover glass; and the preparations were allowed to stand for at least a week before measurements were made, in order that the material might come into equilibrium with the mounting medium. To avoid differences resulting from variations in the length of the uncoiled basal part of the conidium, the first measurements (table IX) were made across the diameter

TABLE IX

Measurement classes	*Helicoma Mülleri*				*Helicoma Curtisii*		
	Number of spores in				Number of spores in		
	Maple	Birch	Chest-nut	Pot. D. agar	Swamp ash	Birch	Pot. D. agar
12.6 μ	1	—	—	8	2	—	3
14.4 μ	7	5	—	48	20	27	22
16.2 μ	16	15	8	45	20	23	22
18.0 μ	20	9	27	1	2	—	3
19.8 μ	—	—	12	—	—	—	—
21.6 μ	—	—	3	—	—	—	—

of the entire spore, at right angles to the point of attachment. The thickness of the spore filament, as shown in table X, was measured opposite the point of attachment of the spore. The

TABLE X

Measurement classes	*Helicoma Mülleri*				*Helicoma Curtisii*		
	Number of spores in				Number of spores in		
	Maple	Birch	Chest-nut	Pot. D. agar	Swamp ash	Birch	Pot .D. agar
3.6 μ	3	8	12	—	—	1	6
4.5 μ	14	11	23	4	9	7	21
5.4 μ	23	8	15	25	34	34	22
6.3 μ	1	—	—	4	7	8	1
7.2 μ	—	—	—	1	—	—	—

results of these measurements show that for *Helicoma Mülleri* there is a slight difference in size between material from agar and from bark; that on maple, birch, and chestnut barks the greater number of spores are from 16.2 to 18.0 μ in diameter, on agar the

average number is greatest at 14.4 μ, and from that point they vary toward the smaller diameter. With *H. Curtisii*, the material from swamp ash and birch bark showed little variation from that on agar. In both species, the width of the conidial filaments varied but little, the greatest variation being shown by the spores of *Helicoma Curtisii* grown on the artificial substratum, but here the difference is only one micron and therefore is of little taxonomic interest. Similarly, when the number of coils, shown in table XI, and the number of septa, table XII, are compared,

TABLE XI

Number of coils	*Helicoma Mülleri*				*Helicoma Curtisii*		
	Number of spores in				Number of spores in		
	Maple	Birch	Chestnut	Pot. D. agar	Swamp ash	Birch	Pot. D. agar
1	1	—	—	—	—	—	—
1¼	4	—	—	4	2	—	2
1½	15	19	21	30	24	23	19
1¾	23	11	26	8	24	27	27
2	5	3	3	—	—	—	—

TABLE XII

Number of septa	*Helicoma Mülleri*				*Helicoma Curtisii*		
	Number of spores in				Number of spores in		
	Maple	Birch	Chestnut	Pot. D. agar	Swamp ash	Birch	Pot. D. agar
6	2	—	—	2	5	5	1
7	—	1	—	8	11	15	11
8	14	7	2	21	28	28	32
9	18	13	16	19	—	—	4
10	4	5	18	2	—	—	—
11	—	1	12	—	—	—	—
12	—	—	3	—	—	—	—
13	—	—	1	—	—	—	—

they are found to be quite constant in both species. It is evident, then, that these characters, supplemented by other peculiarities in the shape of the spores and spore filaments, are of decided value in the taxonomic treatment of this group of fungi.

HUMIDITY

The Helicosporeae require a relatively high degree of humidity, their habitat being the moist under-side of wood or bark, or even

on twigs partly buried in leaves. However, one of the species here considered, *Helicoma Curtisii*, appears to be capable of maintaining its existence in relatively dry situations. This species is not infrequently found growing under the dead bark of standing apple trees, in which situation it is subjected to a degree of desiccation during the summer months. Yet, while the species appears to be resistant to drought, for continued growth a high degree of humidity is a prerequisite, as will be seen later.

The seasonal occurrence also is correlated with the moisture requirements of these fungi. Although many may be found during the summer months in moist habitats, a number are found more frequently and in better condition as regards vegetative growth and spore production, in the spring and fall months.

The importance of humidity to the germination and growth of the organisms is clearly shown by the following experiments in which the moisture requirements were determined under controlled conditions by the method previously used by the writer:[1] In the bottom of van Tieghem cells was dropped a definite amount of sulphuric acid, the concentration of which varied according to the degree of relative humidity desired. The conidia were sown on potato-dextrose agar that had previously been placed on the under-side of a sterilized cover glass, which in turn was sealed to the cell by vaseline.

The spores of all species germinated readily at 100 per cent relative humidity. The percentage of germination and the length of time required for the process varied, as is to be expected, with the species. For example, 65 per cent of the spores of *Helicoma Mülleri* germinated in 24 hours and 96 per cent at the end of 48 hours; of the spores of *Helicosporium aureum*, 21 per cent germinated in 48 hours, and 88 per cent in 96 hours. The spores of the remaining species germinated in a similar fashion, the number producing germ tubes increasing with time until nearly all had germinated. Below 100 per cent relative humidity, there was a rapid falling off in the number of germinating spores. In fact, 98.8 per cent relative humidity appeared to be the lower limit, while at or below 95 per cent the conidia became plasmolyzed. The conidia of *Helicoma Mülleri*, *H. Curtisii*, and

[1] Linder, D. H. *l. c.*

Helicosporium gracile were the only ones that germinated at 98.8 per cent humidity. In this amount of moisture, 6.8 per cent of the spores of *Helicoma Mülleri* had produced germ tubes at the end of 48 hours; 4 per cent of those of *Helicoma Curtisii* had germinated in 96 hours; while in the case of *Helicosporium gracile* only a fraction of 1 per cent germinated in a month. In the last species, those spores that did germinate had changed considerably in appearance. The cells, as shown in pl. 14, fig. 11, had become deeply colored and greatly swollen between the septa, while only very short germ tubes were produced. The remainder of the species, with the exception of *Helicoon sessile,* remained turgid at 98.8 per cent relative humidity, although they did not germinate until again placed in an atmosphere of 100 per cent relative humidity. *Helicoon sessile,* however, proved to be extremely sensitive to changes in humidity, for at 98.8 per cent some of the cells of most of the spores were plasmolyzed; at lower degrees of humidity all were plasmolyzed.

In a previous paper it was stated by the writer[1] that "spores failed to germinate unless the humidity was above 49 per cent, while with the spores that germinated before the cell came into equilibrium, presumably because of the large amount of agar surrounding the spores, growth soon ceased . . . . ."

Since the more recent studies have demonstrated the fact that the other species of the Helicosporeae require a greater amount of moisture in which to germinate, the experiments with *Helicodesmus albus,* synonymous with *Helicodendron triglitziensis,* were repeated with smaller van Tieghem cells, less agar, and a greater amount of the sulphuric acid solutions in the bottom of the cells. The results show quite definitely that a higher degree of humidity than that previously stated is required for germination, the minimum being 98.8 per cent relative humidity.

The resistance of the conidia of different species to drying is extremely variable. The spores of *Helicoon sessile*, for example, when maintained at 97 per cent humidity for one week and then transferred to 100 per cent relative humidity, showed only 5 per cent of germination after 4 days, whereas 41 per cent of the spores of freshly collected material transferred directly to cells main-

[1] Linder, D. H. *l. c.*

tained at 100 per cent humidity germinated in 2 days. This species, however, is the most sensitive to the effects of drying. Spores of *Helicoma Mülleri*, on the other hand, when kept in a van Tieghem cell at 49 per cent relative humidity for two weeks and then transferred to 100 per cent relative humidity, germinated to the extent of 37 per cent at the end of 24 hours, and 66 per cent at the end of 48 hours. Thus, although there was lag in germination, the increase in the percentage in the spores exposed to conditions of severe drought for two weeks is approximately the same as that in spores from newly collected material transferred directly into cells maintained at 100 per cent relative humidity. It appears, therefore, that short exposures to drought has little effect on the viability of spores of certain species. When, however, spores were kept for nine months at the humidity and temperature of the laboratory, the results are quite different. Thus, spores of *Helicoma Mülleri*, *Helicosporium aureum*, and *H. gracile* did not germinate at the end of that period; those of *Helicoma Curtisii* and *Helicomyces scandens* did so even after eleven months, the former, however, only germinating to the extent of 4.8 per cent.

Vegetative growth is limited by the same conditions of humidity as is spore germination. This was shown by allowing spores to continue growth four days after germination in a saturated atmosphere, after which they were transferred to van Tieghem cells kept at relative humidities of 93–98.8 per cent. The growth of the mycelium was then measured at intervals.

Just as the conidia of the different species failed to germinate, so did the mycelium fail to continue growth below 98.8 per cent relative humidity. At this degree of humidity growth, when it did take place, was extremely slow. As an instance, the original germ tubes of *Helicoma Mülleri* made but little growth at 98.8 per cent relative humidity, even though measured at the end of thirty days. The original cells of the hyphae, as is shown by pl. 21, fig. 20, had become enlarged and rounded and new branches were produced. In these new branches the protoplasmic content appeared much denser and more highly refractive than that of the first-formed germ tubes, and the walls were less conspicuously bulging between the septa. This reaction to a dry environment, namely, the enlargement of the original cells and the production

of new branches with dense protoplasm, is characteristic of the majority of the species studied here. *Helicoma Curtisii* proved an exception, as vegetative growth was able to continue at a slightly lower degree of humidity than could spore germination. It was found that at 98.9 per cent relative humidity there was a definite growth of the original germ tube. At 97 per cent relative humidity growth of the original germ tube had been checked, but new hyphae, carrying on growth, were produced, while at 96 per cent relative humidity the original germ tubes had for the most part plasmolyzed and the new hyphae that had been produced grew at the expense of the original and then but very slowly. Although they were not measured, the hyphae of the crowded spores made better growth than did those that were isolated. Below 96 per cent relative humidity the germ tubes were plasmolyzed and no new hyphae were found. These results confirm the observations made from naturally growing material and indicate that, although the fungus requires very moist conditions for germination, once it has become established it may grow under a wide range of conditions.

From the preceding, it is evident that humidity is one of the very important factors in determining the growth and distribution of members of this group. Indeed, none of the species proved capable of continuing growth below 95 per cent relative humidity. Yet, in spite of the fact that on potato-dextrose agar in van Tieghem cells such very moist conditions are required, it does not appear to the writer that the limits of vegetative growth as thus shown are so fixed under natural conditions. Such factors as porosity of the substratum and abundance of capillary water must be considered. With these two factors favorable, as they are likely to be on the natural substratum, it would appear that moisture would be more readily available, even at lower degrees of atmospheric humidity than it is in van Tieghem cell cultures. Furthermore, it should be pointed out that in these cell cultures any moisture that might result from the metabolism of the organism is immediately absorbed by the sulphuric acid in the bottom of the cells. Therefore, these experiments, while indicating growth limits in a highly artificial environment, should

not be considered absolute, but rather as indicating general high-humidity requirements.

Similar allowances should also be made when the relation of humidity to germination of the spores is considered. Since the spores resting on the surface of the substratum are in less intimate contact with it, the experimental figures may prove a little higher than they actually are in nature. Nevertheless, they do indicate that a high degree of humidity is essential to germination. Similar experiments made by Zeller[1] with wood-destroying members of the Basidiomycetes also make this point clear, since, although in his trials he obtained a relatively small percentage of germination at as low as 63 per cent humidity, still the higher percentages of germinations were found to be correlated with the point of saturation of the wood fibres.

TEMPERATURE

In their natural environment these fungi, occurring as they do in moist shaded habitats, are for the most part protected from high temperatures. Furthermore, certain species, such as *Helicoma Mülleri*, *H. Curtisii*, and *Helicomyces scandens*, appear to be most abundant in the early spring, while *Helicodendron tubulosum* and *H. triglitziensis* occur in the late fall. The first two species are also found in the summer when conidia are produced abundantly, although but slightly more so than when found in March just after the snows had disappeared. *Helicomyces scandens*, however, appears during a more limited period, generally from the first of April until the middle of June in temperate regions. *Helicodendron tubulosum* and *H. triglitziensis* were found by the writer in relative abundance only in October and November, the same time of the year, apparently, that they occur in Europe. Such a seasonal appearance strongly suggested a correlation in certain species at least, between temperature and growth. To determine this point and also to discover other effects of temperature, the following experiments were performed.

In these experiments, the fungi were started on potato-dextrose agar at laboratory temperature. The radii of the colonies were

[1] Zeller, S. M. Humidity in relation to moisture imbibition by wood and to spore germination on wood. Mo. Bot. Gard. Ann. 7: 51–74. 1920.

measured at the end of 6 days, and the cultures were divided, one set placed in an ice-box that was maintained at 11° C., one in an incubator at 26° C., and another in an incubator that varied between 21 and 22° C. The figures derived from this work represent an average of three series at each temperature.

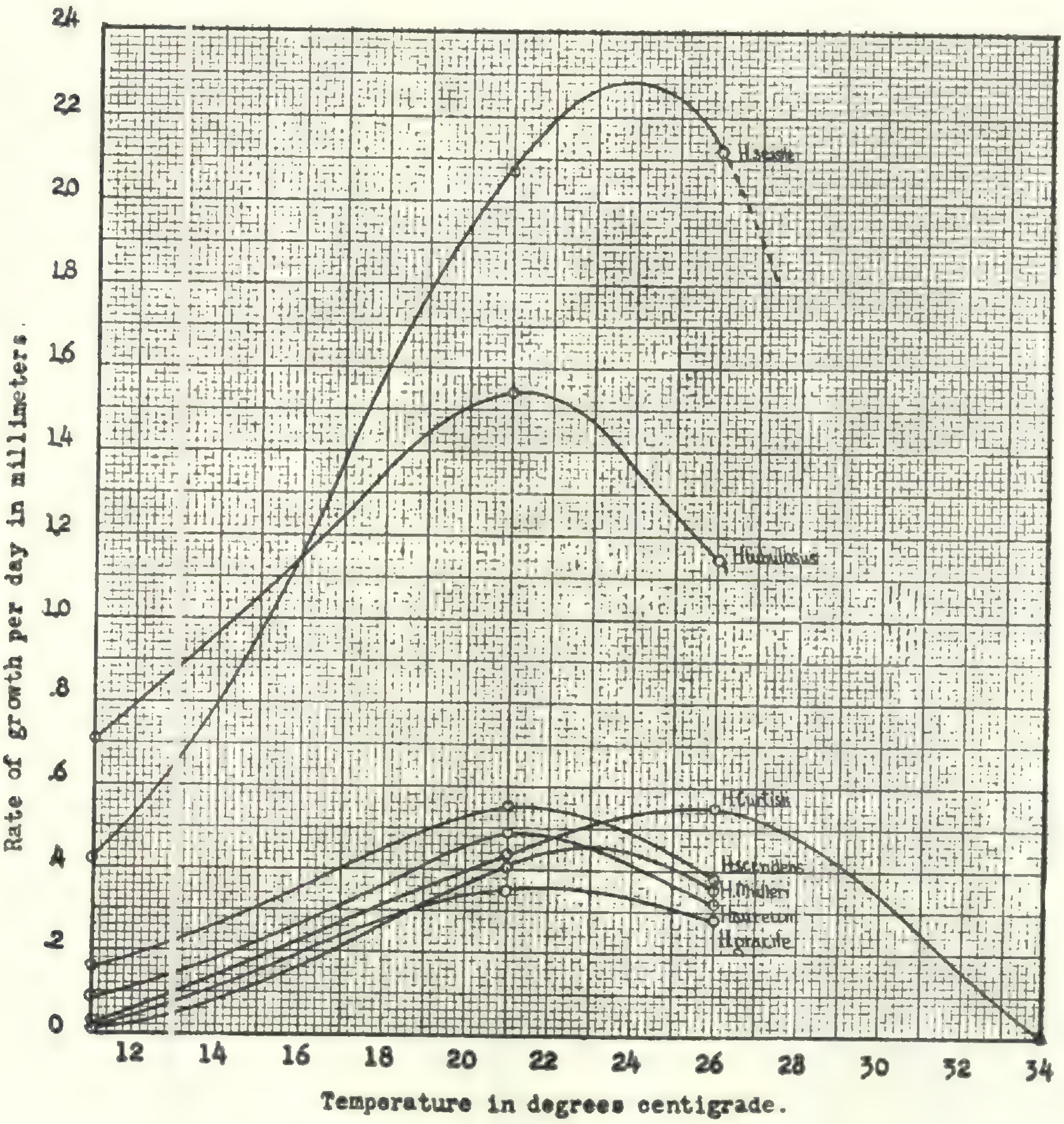


Fig. 2. Effect of temperature on rate of growth.

The results obtained show that the optimum range of temperature is between 21 and 26° C., as is shown graphically in the accompanying curves based only on three points of observation (four in the case of *H. Curtisii*) but constructed to correspond

with those of Fawcett.[1] These figures are slightly lower than those indicated for *Fusarium* spp., *Pythiacystis*, *Phytophthora*, *Diplodia*, *Phomopsis*, and most of the species of *Rhizopus*, since, as has been shown by the work of Tisdale,[2 3] Fawcett,[4] and Weimer and Harter,[5] the optimum temperature for growth of the species of those genera is between 24 and 30° C.

Production of conidia cannot always be correlated with maximum growth, although in the species studied here there is, in the majority of cases, such an agreement. *Helicoma Mülleri* produced spores equally abundantly at 11 and 21-22° C., although the rate of growth is .012 and .413 mm. (maximum) per day. *Helicodendron tubulosum* produced spores only at 11° C. and then not abundantly. When, however, cultures that were growing in the laboratory were exposed to freezing temperatures, −2.2 to −6.6° C., and then brought back into room temperature, spores were produced in abundance. *H. triglitziensis* behaved in a similar fashion, although it was previously stated[6] that "culture experiments indicate clearly that conidium production is dependent on exposure to sunlight . . ." When this species was again studied in the recent comparative work, sunlight apparently had little effect on sporulation unless the material had been exposed to freezing conditions and then returned to the temperature of the laboratory. It thus seems that cold has a marked effect and that the previous history of the cultures was not sufficiently considered, since the inoculum for the experiments on the effect of light came from test-tube cultures that had been left out of doors during the months of January, February, and March. Such a relation between sporulation and temperature would explain the occurrence of the fungi in October and November, at which time the organisms are subjected to low temperatures, or even frost, at night, and higher temperatures during the day.

[1] Fawcett, H. S. The temperature relations of growth in certain fungi. Univ. Cal. Publ. Agr. Sci. **4**: 183–232. 1921.

[2] Tisdale, W. B. Relation of temperature to the growth and infecting power of *Fusarium lini*. Phytopath. **7**: 356–360. 1917.

[3] ———, Influence of soil temperature and soil moisture upon the Fusarium disease in cabbage seedlings. Jour. Agr. Res. **24**: 55–95. 1923.

[4] Fawcett, H. S. *l. c.*

[5] Weimer, J. L., and L. L. Harter. Temperature relations of eleven species of *Rhizopus*. Jour. Agr. Res. **24**: 1–40. 1923.

[6] Linder, D. H. *l. c.*

The effect of freezing temperatures on the viability of the conidia is noteworthy, since asexual spores have been considered as a means of dispersion of species under favorable circumstances. As had already been pointed out in the case of *Helicodesmus albus* (*Helicodendron triglitziensis*), both conidia and mycelium are capable of surviving periods of cold without the aid of an asexual spore form. In the present experiments, cultures were exposed for three days to temperatures never higher than −2.2° C., and as low as −6.6° C. This exposure, though brief, did not impair the vitality of the spores. On the contrary, it increased the percentage of germination of the spores of *Helicoma Mülleri* from 96 to 98.5 per cent; of *H. Curtisii* from 28 to 94 per cent; and of *Helicoon sessile* from 41 to 92 per cent.

The color of the colonies of some species is also affected when grown at different temperatures. In fact, temperature appears to cause almost as conspicuous a change in color as does the presence or absence of a suitable carbohydrate material. *Helicosporium gracile*, when grown at 11° C., is "Dark Olive Buff" tinged "Olive Yellow" by the presence of the light yellow spores; at 21° the color of the colony is much the same except that it is lighter on account of more numerous spores; but at 26° the colony is "Light Brownish Olive." Colonies of *Helicosporium aureum* are "Smoke Gray" at 11° C., while at 21 and 26° C. they are "Citrine Drab" with a "Dark Olive Buff" periphery. *Helicoma Curtisii* and *Helicomyces scandens* also vary in color with differences in temperature, the former being "Water-Green" at 11° C., and "Lincoln Green" with an appressed almost colorless periphery at 21° C. or a buff-colored periphery at 26° C.; the latter species is "Deep Grayish Olive" with appressed mycelium at 11° C., lighter in color because of the more numerous conidia at 21° C. and almost black with a hyaline outer fringe at 26° C. The color of the colonies of the remaining species varied to some extent with changes in temperature, but not so conspicuously. Thus it is shown that temperature may be an additional factor in determining the color of the colonies of these species.

HYDROGEN-ION CONCENTRATION

In a comparative study of the growth of a group of fungi on artificial substrata, hydrogen-ion concentration is a factor that

must be taken into consideration, since it may cause changes in rate of growth and in the coloration of the colonies. These investigations therefore were undertaken primarily in order to dis-

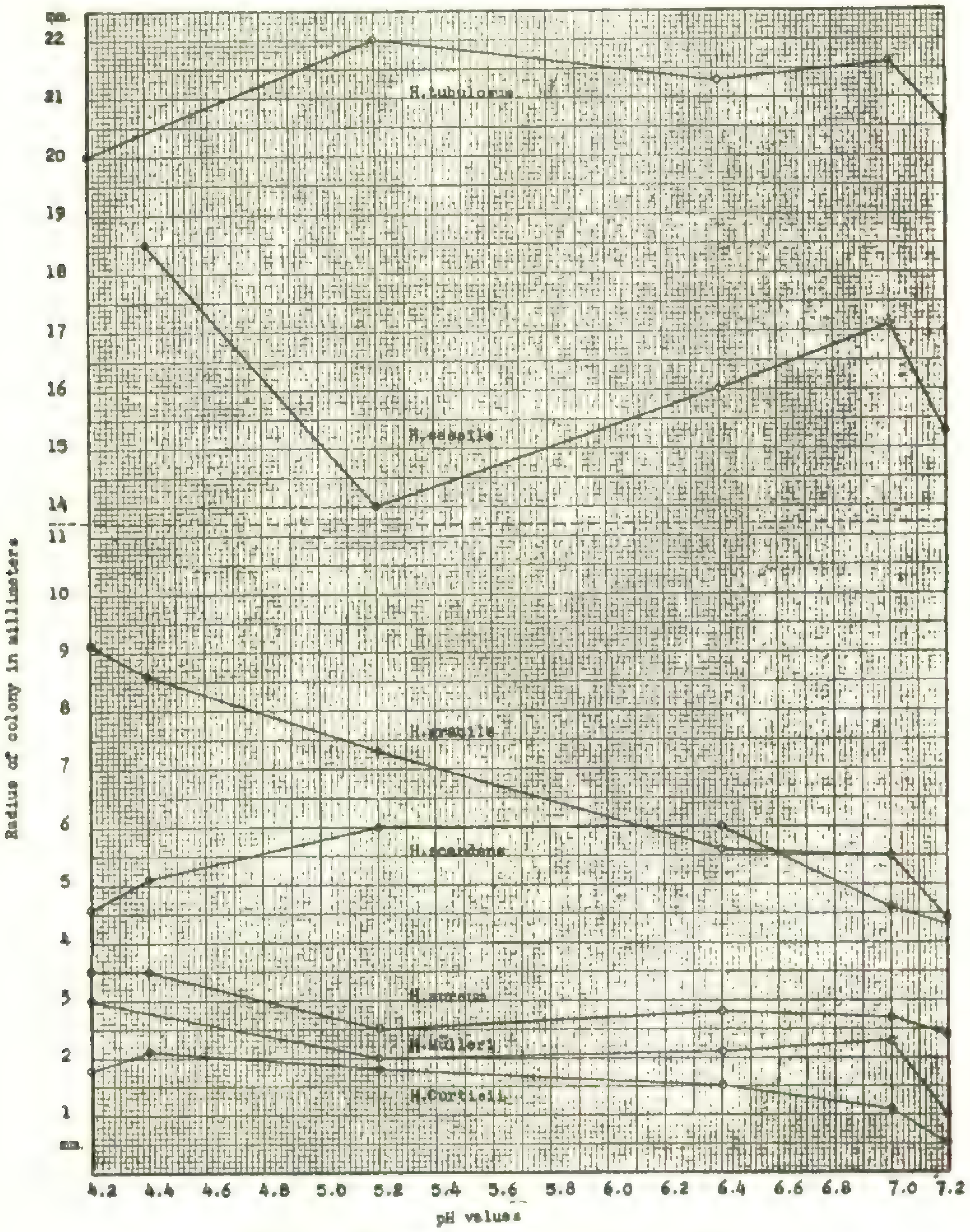


Fig. 3. Effect of hydrogen-ion on growth.

cover what influence, if any, changes in hydrogen-ion concentration of the substratum might have on the color of the fungi. In this respect the work proved somewhat disappointing, for, in

general, no differences were noted. *Helicoma Curtisii*, however, was an exception, since it reacted rather strongly in coloration to changes in acidity. Colonies started at pH 4.4 developed a fluffy mycelium which at the end of twenty days was "Light Yellowish Olive" at the center, shading to "Olive Yellow" at the periphery. In the colonies started at pH 5.2–7.2, the mycelium at the end of the same period was appressed and hyaline. To a lesser degree, *Helicosporium gracile* also showed changes in color, from "Sepia," the shade present from 4.2–7.0, to "Isabella Color" at 7.2.

By reference to the accompanying graph it will be observed that the points of maximum growth vary with the species, some of them occurring at the point of neutrality, others on the acid side of it, but none on the alkaline side. It seems probable that had it been possible to maintain the agar substrata at a more uniform hydrogen-ion concentration during the experiments there would be a sharper dropping off in the curves at or slightly on the acid side of neutrality. As it was, those cultures started at 7.0 and 7.2 tended to become acid, 6.6 and 6.8. In general, these results agree with those found by Wolpert[1] in the growth of various wood-destroying Basidiomycetes and indeed with the findings of other workers in the case of *Penicillium* among the Fungi Imperfecti, and the imperfect stage of *Sclerotinia*. On the contrary, vigorous plant pathogens, such as *Fusarium* spp., etc., according to the tabulations of Macinnes,[2] apparently find neutral or basic conditions more favorable for growth.

Summary

1. In these investigations, representatives of five of the seven genera of the Helicosporeae in the order Moniliales of the Fungi Imperfecti have been studied comparatively. Their life histories and their reactions under controlled conditions of environment have been noted.

2. The study of the life histories of these forms brings out the fact that in *Helicoma*, *Helicomyces*, and *Helicosporium* the spores

[1] Wolpert, F. S. Studies in the physiology of fungi. XVII. The growth of certain wood-destroying fungi in relation to the H-ion concentration of the media. Mo. Bot. Gard. Ann. **11**: 43–97. 1924.

[2] Macinnes, Jean. The growth of wheat scab organism in relation to hydrogen-ion concentration. Phytopath. **12**: 290–294. 1922.

possess hyaline or colored outer sheaths, and exospores which rupture as the spores swell in preparation for germination. So far as the writer is aware, this is the first time such structures have been reported in this group. It was also found that in the early stages, germination of the spores took place in two ways: 1, by the simple elongation of the terminal cells to form a hypha; 2, by the lateral production of germ tubes, chiefly from the central cells of the spore filaments. *Helicosporium gracile* germinates typically by the first method, and *Helicoma Curtisii* and *H. Mülleri* frequently do. The other species generally follow the second method of germination.

3. Heretofore, relations between the perithecial and conidial stages have been inferred from the presence of the two forms together. By pure, single-spore cultures, the perfect stage, *Lasiosphaeria pezizula*, was definitely shown to be connected with *Helicoma Curtisii.*

4. Polymorphism appears to be less frequent than was formerly supposed, and the life histories of the species more simple. Among the species studied in this part of the paper, only one, *Helicosporium aureum*, was found to produce more than one type of asexual spore, and that but very rarely.

5. When the fungi were grown on Schmitz's solution to which were added separately 4 per cent of maltose, wheat starch, pectin, xylose, cellulose, and asparagin, it was found that, considering both the amount of spores and vegetative hyphae produced, pectin and cellulose proved, in general, to be the most favorable sources of carbohydrate material. The other carbohydrates also played an important part in supplying nourishment for vegetative activity. Asparagin was utilized to but a small extent.

6. The fungi were found to be very dependent on the existence of a high degree of humidity for growth and germination. Not one of the species was able to germinate when conditions were under 98 per cent relative humidity, nor to continue vegetative growth under 96 per cent. Exposure to drying had different effects on the germination of the spores of different species. Spores of *Helicoon sessile* lost some of their vitality when exposed to an atmosphere kept at 97 per cent relative humidity. Other spores proved more resistant; those of *Helicoma Curtisii* and *Helicomyces*

scandens germinated after exposure of 11 months to the even drier conditions of the laboratory.

7. The optimum temperature for the growth of members of the group was found to be between 21 and 26° C., while sporulation was favored by cooler temperatures, especially in the case of *Helicosporium gracile, Helicodendron tubulosum*, and *H. triglitziensis*.

8. All species grew best in media that were acid or neutral. There was a rapid decrease in growth between Ph 7.0 and 7.2.

9. Factors influencing the color of the colonies on artificial substrata are type of carbohydrate present, temperature, H-ion concentration, and to a lesser extent the degree of relative humidity.

Part II. Taxonomic Treatment

This monographic study represents an attempt to bring order out of the chaos existing in the helicosporous Fungi Imperfecti. In studying those species already described an endeavor has been made to consult as many of the types as possible, and in this respect the writer has been extremely fortunate for only a few remain unstudied. Where types have been lacking, the original descriptions and illustrations have been sympathetically studied with the purpose of correlating those species with the material at hand. In spite of painstaking care there remain a few species whose identity is still doubtful.

In arranging the forms presented here, an attempt has been made to violate as little as possible the Saccardan system of classification while at the same time applying Morgan's system consistently. This latter system, based on the morphology of the spores, was decided on as a result of the study of the several species in culture and a greater number as they occur in nature. In the cultural experiments, as has already been pointed out, the color of the fungus, upon which the Saccardan system is based, varies with changes of environmental factors. In addition, it becomes clear from the study of a large number of species growing in their natural habitats that the age of the colonies also has a marked influence on the color. Thus we find that conidiophores of *Helicosporium lumbricoides* when young are hyaline but with age become deep fuscous. The color of the colonies changes ac-

cordingly from light gray to sepia. On the other hand, *Helicomyces scandens* both on the natural and the artificial substrata produces hyaline mycelium at first, but with age the creeping portions and the base of the short upright conidiophores become dilute fuscous or even a deeper shade, while the spores, at first white in mass, become pinkish and finally brownish. With the color so variable, it has seemed advisable to neglect the lines dividing the Dematiaceae and the Mucedinaceae and to combine the species in groups based on the morphological characters of the conidia. This step is not unprecedented, as will be evident from a perusal of works on the genus *Aspergillus*, in which fuscous spore forms are classified along with the non-fuscous ones without regard to the artificial lines created by the families Mucedinaceae and Dematiaceae. This practice has much in its favor, and the adoption of it generally would do away with much useless synonymy and the separation of obviously related forms.

The perfect stages of these fungi, as has been intimated earlier, are but rarely found and but few have been definitely connected with their imperfect spore forms. In the present work the writer has endeavored to collect all previous records of complete life histories and to test their veracity. It is thus hoped that more interest will be aroused in connecting the sexual and asexual stage and that out of this increased knowledge we may eventually obtain a better system of classification and a clearer idea of the phylogeny of the group. In the past, interest has been centered in only one or the other of the forms, and whereas one might have been adequately described, the other was generally neglected. On the basis of our present knowledge, it may be said, for the genera *Helicoma* and *Helicosporium* at least, that the conidial stage is correlated with the phragmosporous type of simple Sphaeriae, especially with the genera *Lasiosphaeria*, *Chaetosphaeria*, and *Acanthostigmella*. As for the problems of nomenclature that arise when the two phases in the life histories of these forms have been correlated, the writer has avoided changing the names of either for two reasons. In the first place, the names of such forms have become established in the literature and in general usage. To juggle them again increases the already-long list of synonyms without obtaining any advantages. Secondly, the

occurrence of the two stages together is so rare that it is necessary to have a separate system of classification for the perfect and imperfect forms. There appears to be little hope of avoiding such a bilateral system for some time to come. After all, it makes little difference whether we call the perfect stage of *Helicoma Curtisii*, *Lasiosphaeria Curtisii* or *L. pezizula* so long as we know the relations to be true, since *Lasiosphaeria* must still be classified among the Sphaeriaceae of the Ascomycetes and *Helicoma* in the Dematiaceae of the Fungi Imperfecti. In such cases it seems the technicalities of nomenclature should not be made a fetish.

The geographical distribution of the members of this group is indeed varied. Many species are to be found in North America and Europe, as is shown by a number of species among which *Helicoma Mülleri*, *Helicomyces roseus*, *Helicodendron tubulosum*, and *Helicomyces scandens* may be mentioned. The last named has also been collected in Chile. *Helicoma fasciculatum* and *H. simplex* appear to be confined to the Orient, although the former species has been reported from California. *Delortia palmicola* has been collected by the writer in tropical South America and in Africa. Cases of endemism, however, are not infrequent. *Xenosporella Thaxteri* and *Helicoma conicodentatum* have been collected respectively only in Trinidad and Grenada. The genus *Drepanoconis*, with two species, appears to be confined to South America, while the monotypic genus *Helicostilbe*, as emended in this paper, is confined to India. At present, our knowledge of the distribution of the members of this group is at best fragmentary, since too few collections have been made to allow the accurate mapping of their ranges.

In studying specimens, the writer has found it necessary to make microscopic preparations. The most satisfactory ones are made by sectioning the specimens as they occur on the substratum. When the species is an inhabitant of decaying wood, it has proved best to section the wood with the grain. Frequently, however, collections were so meager that it was more practical to employ a small, well-sharpened scalpel in order to remove, under a hand lens, a small portion of the specimen with a bit of the substratum. Material thus obtained was mounted in alcohol,

placed under a cover glass, and then eosin-glycerine was allowed to run into the specimen as the alcohol evaporated. A more satisfactory and more rapid medium was found in lacto-phenol as used by Sartory.[1] This not only swelled the material, but, if a small quantity of cotton blue were added, stained it at the same time. Permanent preparations were made by allowing such mounts to stand until the water in them had evaporated, a matter of a week or more, and then they were sealed by ringing with King's Amber Cement.

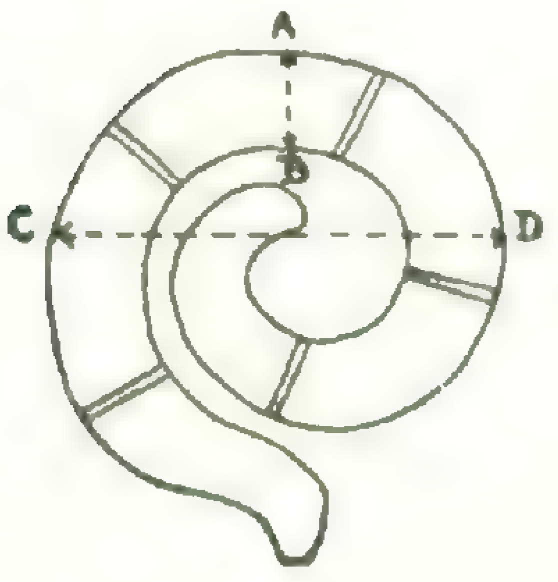


Fig. 4.

On all possible occasions a large number of measurements were made of each species in order to observe variations in size. In measuring conidia, it has been found necessary to adopt more or less fixed standards. The diameter of the coiled conidia was measured at right angles to the point of attachment, along the line c–d of the accompanying figure. The width of the conidial filament was measured opposite the point of attachment along the line a–b. On occasions when the spore was more than two- or three-times coiled, the outer and the middle coil were measured. Colors when given in quotation marks are those of Ridgway's 'Color Standards and Color Nomenclature,' Washington, 1912.

Citations have been kept as brief as possible and at the same time sufficiently ample for the identification of the material studied. The abbreviated names of the herbaria will be found in parentheses following the citations. The following is a list of abbreviations used:

- B = Herbarium of the Botanical Museum, Berlin-Dahlem.
- BM = Herbarium of the British Museum (Natural History), S. Kensington, England.
- F = Farlow Herbarium, Harvard University, Cambridge, Massachusetts.
- H = Herbarium of the University of Helsingfors, Helsingfors, Finland.
- Ia = Herbarium of the University of Iowa, Iowa City, Ia.

[1] Sartory, A. Guide pratique des manipulations de mycologie parasitaire. p. 100. Paris, undated.

K = Kew Herbarium, Kew Greens, Surrey, England.
L = The writer's herbarium.
MBG = Herbarium of the Missouri Botanical Garden.
NY = Herbarium of the New York Botanical Garden, Bronx Park, New York.
NYS = Herbarium of the New York State Museum, Albany, N. Y.
P = Herbarium of the Museum of Natural History, Paris.
Pe = Herbarium of the Royal Botanic Garden, Peradeniya, Ceylon.
S = Herbarium of the Royal Botanical Museum, Stockholm, Sweden.

Key to Genera

1. Conidiophores forming a loose arachnoid, cottony or velvety colony, or else apparently obsolete, not forming a compact fruiting body (MUCEDINACEAE and DEMATIACEAE)....3
1. Conidiophores aggregated to form a compact structure....2
2. Conidiophores aggregated to form a stele upon which the spores are borne acrogenously (STILBACEAE)....*Helicostilbe* (p. 333)
2. Conidiophores aggregated to form a flattened pulvinate or irregularly globose fruiting body (TUBERCULARIACEAE)....10
3. Conidia coiled in three planes to form a cylindrical or barrel-shaped spore body.4
3. Conidia coiled in two planes, or if in three planes then not as above....5
4. Conidia in chains....*Helicodendron* (p. 329)
4. Conidia not in chains....*Helicoon* (p. 322)
5. Parasitic on vascular plants; conidiophores obsolete or as swellings of the vegetative hyphae; spores toruloid....*Gyroceras*
5. Saprophytic or some doubtfully parasitic on other fungi; conidiophores present, in some not conspicuous but then spores are not toruloid....6
6. Conidial filaments thick in proportion to their length, not hygroscopic....7
6. Conidial filaments thin in proportion to their length, hygroscopic....9
7. Conidia in chains....*Helicodendron* (p. 329)
7. Conidia not in chains....8
8. Conidia longitudinally and transversely septate....*Xenosporella* (p. 317)
8. Conidia transversely septate....*Helicoma* (p. 295)
9. Conidiophores and conidia hyaline; the conidiophores as teeth on, or short erect branches from, the creeping vegetative mycelium....*Helicomyces* (p. 270)
9. Conidiophores or conidia or both some shade of fuscous; conidiophores conspicuous....*Helicosporium* (p. 275)
10. Sporodochia effuse-pulvinate, at first covered by epidermis of host, then erumpent; conidia once-coiled with thick hyaline walls..*Drepanoconis* (p. 341)
10. Sporodochia pulvinate to irregularly globose, dry, horny, or gelatinous; conidia without a conspicuously thickened wall....11

11. Conidia coiled in three planes to form a conical or oblong-ellipsoidal spore body.. *Troposporium* (p. 345)
11. Conidia not coiled in three planes, or if so then the filaments irregularly twisted and contorted..12
12. Conidia once-coiled, 1–3-septate; fructifications gelatinous...*Delortia* (p. 338)
12. Conidia not 1–3-septate, or if so then sporodochia not gelatinous........13
13. Conidial filaments 7 μ or more in width; conidia coiled in three planes, twisted and contorted................................*Hobsonia* (p. 339)
13. Conidial filaments less than 7 μ in width; conidia not coiled in three planes....14
14. Conidiophores slender, even; fructifications horny when dry..*Everhartia* (p. 335)
14. Conidiophores moniliform; fructifications not as above..*Troposporella* (p. 334)

HELICOMYCES

Helicomyces Link, Ges. Naturforsch. Freunde Berlin, Mag. **3**: 21. *pl. 1, fig. 35.* 1809; Wallroth, Fl. Cryptogam. Germaniae **2**: 147–148. 1833; Saccardo, Syll. Fung. **4**: 233. 1886 (in part); Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 39. 1892 (in part); Lindau, in Engl. & Prantl, Nat. Pflanzenfam. **1** (1**): 451. 1900; Lindau, in Rabenhorst, Kryptog. Fl. Deutschl., Öst. u.d. Schweiz **1**^{8}: 533. 1906.

Type species of the genus is *Helicomyces roseus* Link.

Conidia hyaline, white to pinkish in mass, the filaments slender, hygroscopic, convolutely coiled to form a disc-shaped body. The conidiophores present as teeth on the repent mycelium or as short erect, hyaline branches. Colonies effuse.

This genus as defined by Saccardo has in the past been a meeting place for all species in which the spores and conidiophores are hyaline, and thus came to include species with non-hygroscopic, relatively thick conidial filaments which have been transferred to *Helicoma;* species with the filaments coiled in three planes to form an ovoid spore body which have been placed in *Helicoon;* while those species with hygroscopic spores, but also with fuscous or dilute fuscous conidiophores, have found a position in the genus *Helicosporium.* The separation of the genera *Helicomyces* and *Helicosporium* is based on the fact that the conidia and conidiophores of the former are hyaline and that the mycelium is repent, not erect or ascending as in the latter. Such species with erect or ascending subhyaline or dilute fuscous conidiophores should be sought for in the genus *Helicosporium.*

KEY TO THE SPECIES OF HELICOMYCES

Colonies effuse, white or grayish to pink, but without bristle-like setae.
Conidial filaments 1.5–5 μ thick, coiled in two planes to form a flat disc.
Sterile mycelium and conidiophores mostly hyaline.
Conidial filaments 2.5–5 μ thick, the basal cell slightly swollen and attached obliquely to the sporogenous teeth................*1. H. roseus*
Conidial filaments 1.5–2.5 μ thick, the basal cell slightly swollen. ....*2. H. tenuis*
Sterile mycelium and conidiophores fuscous or dilute-fuscous....*3. H. bellus*
Conidial filaments 5–7 μ thick, the basal cell truncate, not swollen, coiled in three planes to a flattened helix..............................*4. H. ambiguus*
Colonies effuse, whitish to pink; bristle-like setae present........*5. H. scandens*

1. Helicomyces roseus Link, Ges. Naturforsch. Freunde Berlin, Mag. **3**: 21. *pl. 1, fig. 35.* 1809.

Helicomyces albus Preuss, Linnaea **25**: 725. 1852.

Helicomyces elegans Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 45. *fig. 8.* 1892.

Helicomyces clarus Morgan, *Ibid.* 44. *fig. 7.* 1892.

Plate 12, figs. 5–7.

Colony effused, forming a thin flocculose white to pinkish layer. Sterile mycelium creeping, hyaline or occasionally dilute fuscous below. Conidia hyaline, white to pinkish in mass, on teeth on the repent mycelium or on short erect branches, conidial filament slender, 2.5–4.5 μ, seldom 5.5 μ, in diameter, multiseptate, tapering to a terminal cell swollen at the base, which is generally abruptly rounded and obliquely flattened, irregularly coiled when moist, 2¼–3-times coiled when dry, and then the diameter of the coil is 30–45 μ in diameter.

Growing on seed-pods, decaying wood and bark. Widespread.

The diameters of the spore filaments of this species are extremely variable, from (2)–3.5 to 5.5 μ, but these extremes are the exception rather than the rule, since the majority of conidial filaments are 3–4.5 μ in diameter. Morgan, in his description of *Helicomyces elegans*, states that the spore filaments are 5–6 μ thick but the thickest filaments found by the writer on subsequent examination of material communicated by Morgan to Dr. Roland Thaxter is 4.5 μ. There is a possibility that two species may be combined here, but spore sizes intergrade so that it is impossible

to separate them without additional characters, which, however, appear to be lacking.

Specimens examined:

Exsiccati: Mycotheca Fairmani; Roumeguere, Fungi Gall. Exsicc., 2773; Saccardo, Mycotheca Veneta, 1245; Fuckel, Fungi Rhenani, 80.

England: Bristol, *H. O. Stephens* (K); Forden, *Vize* (K); West Kilbride, on rotten bark of *Fraxinus excelsior*, Oct. 1877, *D. A. Boyd* (BM); Stapleton Grove, Aug. 1845, *C. E. Broome* (BM).

France: *Boudier* (P); Ambert, Puy-de-Dome, July 7, 1900, *L. Breviere*, as *Helicosporium vegetum* (S).

Belgium: Graenendael, Nov. 1883, *C. Bommer & M. Rousseau* (P).

Germany: Eberswater, Oct. 1903, *Lindau* (B).

Austria: Rehgrabenberg, July, 1904, *v. Höhnel, 1118*, as *Helicomyces candidus* (F); Hostrichian, *v. Höhnel* (F); Purkersdorf, July, 1903, *v. Höhnel* (F); Kraustein, *v. Höhnel* (F).

United States:

New York: Lyndonville, *C. E. Fairman* (F).

Ohio: Preston, *Morgan*, as *H. elegans* (F).

Trinidad: *Thaxter* (F).

2. **Helicomyces tenuis** Spegazzini, Mus. Nac. Buenos Aires, Anal. **20**: 423. 1910.

Colonies arachnoid or *effuse*, suborbicular, 5–15 mm. *or more* in diameter; hyphae densely and intricately branched, 4–5 μ in diameter, septate, lax, and minutely papillate, hyaline; conidia filiform, 80–120 x 1.5–2 μ, circinate, terminal cells acute, slightly enlarged and obtuse at the basal cells, densely and minutely guttulate (*obscurely septate*), hyaline.

On putrescent culms of *Arundo Donax*. Lezama near Buenos Aires, Argentine, Nov. 1904. *C. Spegazzini.*

The above description, with the writer's modifications in italics, is translated from the original. This species appears to differ from *H. roseus* only in the smaller diameter of the conidial filament. Whether a colony is arachnoid or pulverulent appears to depend on the amount of spores present and in the length of the conidiophores, characters which vary with environmental conditions. The type has not been seen by the writer.

Specimen examined:
Surinam: Paramaribo, Nov. 7, 1923, *Linder, 346* (F).

3. **Helicomyces bellus** Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 42. *fig. 4.* 1892.

"Effused, forming a thin, flocculose stratum, gray with a pinkish tinge. Hyphae creeping, septate, branched, brownish-hyaline, bearing the spores on minute lateral teeth. Spores linear, hyaline, guttulate, faintly multiseptate, coiled quite regularly 2½–3½ times; the thread 140–180 mic. in length by 2.5–3 mic. in thickness; the inner extremity acute, the outer obtuse.

Fig. 5. *H. bellus.* After Morgan.

"Growing on old wood of Liriodendron, Juglans, etc. The hyphae creep close to the substratum and are nearly concealed by the abundant spores; they are nearly twice as thick as the thread of the spore."

4. **Helicomyces ambiguus** (Morgan) Linder, n. comb.
Helicoma ambiguum Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 49. *fig. 15.* 1892.

Plate 12, figs. 8–9.

Colony effuse, forming a thin flocculose, rose-colored layer ("Cartridge Buff" in dried material). Sterile mycelium hyaline, creeping, septate, and branched. Conidiophores hyaline, erect or bent, simple, septate, 10–30 x 2.5–3.5 μ. Conidia hyaline, acrogenous, multiseptate, the filament 3–5-times coiled in 3 planes, 5–7 μ thick, tapering toward the rounded distal end and

towards the truncate basal end; diameter of the coiled conidium 30–40 μ.

On decaying wood of *Platanus*. Ohio.

This species is quite distinct from *H. roseus* in that the thickness of the conidial filament is greater, the conidia are more pronouncedly coiled in three planes and are attached directly to the conidiophore and not swollen at the base and attached obliquely as in *H. roseus*. The conidiophores, also, are more pronounced in this species, the spores being confined to them and not produced on teeth or extremely short upright branches of the creeping mycelium.

Specimen examined:

United States:

Ohio: Preston, Aug. 2, 188?, *Morgan*, in herb. as *Helicoma apiarium*, TYPE (Ia, slide F, MBG).

5. **Helicomyces scandens** Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 42. *fig. 5.* 1892.

Helicostilbe helicina von Höhnel, Kön. Akad. Wiss. Wien, math.-nat. Kl. Sitzungsber. **111**: 1028–1029. 1902.

Plate 12, figs. 1–4; plate 30, fig. 2; plate 31, fig. 3.

Effused, forming a white to pink, setulose colony. Hyphae creeping over the substratum, or climbing the erect bristle-like setae and forming clusters, hyaline, septate, branched. Conidia slender, filamentous, indistinctly multiseptate, 3–4-times coiled, the filament 1.5–3 μ in diameter; the terminal cells acute, the basal cells obtuse at extremities.

On decaying wood and bark. Widespread.

This species in the young condition resembles *H. roseus*. Not only are the colonies pink and effuse, but also devoid of bristles, or if the bristles are present they are so few and scattered as to pass unobserved. With increasing age, however, the characteristic bristles become more evident and the conidiophores tend to become fasciculate, until in the more advanced stages of development the bristles and conidiophores have become so fasciculate as to take on the stilbaceous appearance which caused von

Höhnel to establish the genus *Helicostilbe.* In view of the fact that all stages from the effuse to the stilbaceous may be present and also because frequently only young material is available for study, the recognition of this genus as originally established, would only lead to confusion. It has therefore been emended and *Helicostilbe helicina* has been reduced to synonymy.

Aside from the presence of the dark bristles in *Helicomyces scandens,* this species may be separated from *H. roseus* by the more slender conidial filament, the lack of the rounded, swollen basal cells and the direct attachment of the conidia to the sporogenous teeth.

Specimens examined:

Austria: Wienerwald, on wood of *Carpinus,* May 11, 1902, *v. Höhnel,* type of *Helicostilbe helicina* (F).

United States:

Massachusetts: Canton, *Linder, 1003* (L); Waverley, June 1, 1891, *R. Thaxter* (F).

Connecticut: New Haven, decaying wood in greenhouse, *R. Thaxter* (F).

Ohio: Preston, on wood of *Carya, Morgan,* TYPE (F and ? Ia).

Missouri: Gray Summit, *Linder* (L, MBG 62347, F).

Chile: Correl, December, *R. Thaxter* (F).

SPECIES IMPERFECTLY KNOWN

Helicomyces albus Preuss, Linnaea **25:** 725. 1852.

"Acervulis effusis, albis; sporis basi adnexis, spiraliter subintortus, albis, episporio nucleo subpartito.

"Habitat in cortice arborum frondosarum."

The above is the original description. There are few details of taxonomic value, although since it is stated that the colonies are effuse and the spores are white and attached at the base, it might be implied that this species is very close to *Helicomyces roseus,* if not synonymous.

HELICOSPORIUM

Helicosporium Nees, Syst. d. Pilze u. Schwämme, 63. 1817; Persoon, Myc. Eur. **1:** 19. 1822 (in part); Fries, E., Syst. Myc. **3:** 354. 1832; Saccardo, Michelia **2:** 29. 1880 (in part); Saccardo, Syll. Fung. **4:** 557. 1886 (in part); Lindau, in Engl. &

Prantl, Nat. Pflanzenfam. I (1**): 487. 1900 (in part); Lindau, in Rabenhorst, Kryptog. Fl. Deutschl., Öst. u. Schweiz, 2nd ed. **1**: 270. 1908 (in part).

Type species of the genus is *Helicosporium vegetum* Nees.

Conidia hyaline, light-colored or fuscous, the filaments slender, hygroscopic, convolutely coiled to form a disc-shaped body. The conidiophores conspicuous, dilute fuscous to fuscous, simple to much branched. Colonies effuse or cottony.

This genus is separated from *Helicomyces* in a purely arbitrary manner on the basis of the presence of elongate and conspicuous conidiophores. Such a basis for delimiting the genus was adopted in order to avoid the necessity of changing a large number of names and at the same time to detract as little as possible from the value of Saccardo's 'Sylloge Fungorum.' Species formerly in the genus *Helicotrichum*, before that genus was emended and placed in the Sarcopodiae by Saccardo, will, for the most part, be found in *Helicosporium* as constituted in this paper. On the other hand, those species with proportionately thick, non-hygroscopic spores, whether hyaline or fuscous, are to be found in the genus *Helicoma* where they form a more or less homogeneous group.

KEY TO THE SPECIES OF HELICOSPORIUM

1. Conidia yellow or greenish-yellow in mass 2
1. Conidia in mass some other color 6
2. Conidiophores fuscous or deep fuscous, at first simple or erect 3
2. Conidiophores dilute fuscous to subhyaline 5
3. Conidia borne on hyaline, bladder-like lateral projections from the conidiophores 4
3. Conidia not borne as above, on minute cylindrical teeth or slender branches . . . . . *1. H. vegetum*
4. Conidiophores 390–650 μ long, 5.4–7.2 μ thick near base, branching above at maturity . . . . . *2. H. aureum*
4. Conidiophores up to 480 μ long, 3.6–4.5 μ thick near base, not branching above at maturity . . . . . *3. H. guianensis*
5. Conidiophores subhyaline to dilute fuscous, pellucid, arising from repent or climbing mycelium . . . . . *4. H. gracile*
6. Conidial filament less than 4.5 μ in diameter 7
6. Conidial filament more than 4.5 μ in diameter 13
7. Conidiophores much branched and anastomosing at frequent intervals 8
7. Conidiophores sparsely branched, or if branched then not anastomosing at frequent intervals 9
8. Colonies velvety, up to 400 μ thick, easily separable from the substratum as loose mats of conidiophores; conidial filaments .9–2 μ thick; coiled conidium 18–25 μ in diameter . . . . . *5. H. lumbricoides*

8. Colonies effuse, short-velvety, up to 200 μ thick, not separable from the substratum as above; conidial filaments 1.8–2.5 μ in diameter; coiled conidia 21–29 μ in diameter.................................*6. H. lumbricopsis*
9. Coil of conidia less than 10 μ in diameter; filament 1–2-times coiled; conidiophores fuscous, at first simple, erect, becoming branched and decumbent and bearing conidia on bladder-like projections..........*7. H. decumbens*
9. Coil of conidia more than 10 μ in diameter; conidiophores subhyaline to dilute fuscous, elongate, slender.....................................10
10. Conidial filaments 1 μ in diameter, conidiophores not much branched below..11
10. Conidial filaments 1.5–2.5 μ in diameter; conidiophores much branched below...12
11. Conidiophores clearly septate, mostly simple, not anastomosing above. ....*8. H. griseum*
11. Conidiophores indistinctly septate, elongate, slender, sparsely anastomosing above..*9. H. pallidum*
12. Conidial filaments 2–2.5 μ thick...........................*10. H. albidum*
12. Conidial filaments 1.5–2 μ thick.........................*11. H. phragmites*
13. Conidial filaments 8–10 μ thick; conidia on stout, simple or branched teeth 3–4 × 4–10 μ......................................*12. H. serpentinum*
13. Conidial filaments less than 8 μ thick...............................14
14. Terminal cells of conidiophores smooth; conidial filament 4.5–6 μ thick ....*13. H. nematosporum*
14. Terminal cells of conidiophores rough; conidial filaments 6.3–8 μ thick ....*14. H. Elinorae*

1. Helicosporium vegetum Nees, Syst. d. Pilze u. Schwämme, 68. *pl. 5, fig. 66.* 1817.

? *Helicotrichum pulvinatum* Nees, Acad. Caes.-Leop. Nova Acta **9**: 246. *pl. 5.* 1818.

? *Helicosporium pulvinatum* var. *effusum* Berkeley, Eng. Fung. Fl. **5**: 335. 1836.

Helicosporium Fuckellii Fresenius, Beitr. z. Myk. **3**: 101. *pl. 13, fig. 55–58.* 1863.

Helicosporium olivaceum Peck, Rept. N. Y. State Mus. **27**: 102. 1877.

Helicomyces olivaceus (Peck) Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 40. *fig. 1.* 1892.

Helicomyces vegetus (Nees) Pound & Clements, Minn. Bot. Studies **9**: 659. 1896.

Plate 13, figs. 1–3.

Colony at first finely hirsute, later somewhat cottony, "Sulphin Yellow" to "Dark Citrine." Conidiophores slender, 30–360 × 3–5 μ, at first erect, rigid, tapering to an acute subhyaline

point, later becoming somewhat flexuous, occasionally anastomosing, and producing short lateral branches below, hyaline when young, elongate, subfuscous at maturity. Conidia hyaline, yellowish or yellowish-green in mass, hygroscopic, at first borne acro-pleurogenously on slender, hyaline branches, later produced only pleurogenously on the lower part of the conidiophores, the filament 1 μ in diameter, 2–4-times convolute, the coiled spore 10–15 μ in diameter.

On decaying wood of deciduous trees, mostly of *Quercus*.

When only a few isolated specimens of *Helicosporium vegetum* in varying degrees of maturity are studied, the species appears to be a complex of many. Thus, study of the type specimen of *H. Fuckelii* demonstrates clearly that the species was described from nearly mature individuals which had given rise to lateral sporogenous branches. In the same collection the simple erect conidiophores typical of the younger stages of *H. vegetum* are also found. *Helicosporium pulvinatum* is apparently based on the very mature, loosely and much-branched condition of this species.

Specimens examined:

Exsiccati: Fuckel, Fungi Rhenani, as *Helicoma Mülleri*.

England: Mochay Lawn, May, 1839 (K); King's Cliffs, *Berkeley* (K); Lynn, on *Fagus*, May, 1872, *C. B. Plowright* (B, S).

France: Villebertin, May 28, 1882.

Germany: Eberbach, *Fuckel*, in Fungi Rhenani, as *H. Mülleri*, the type of *H. Fuckelii;* Triglitz, on decaying oak twigs, Nov., 1907, *O. Jaap*, as *H. pulvinatum* (B); Beinitz, Leipzig, on birch bark, *G. Winter* (B).

Austria: Wienerwald, June 9, 1907, *von Höhnel* (F); Wolfersburg, on *Quercus*, May 28, 1902, *von Höhnel* (F); Aggsbach, May 26, 1902, *von Höhnel* (F); Schacherswal, Redsalpe, June 6, 1900, *von Höhnel*, as *H. pulvinatum* (F).

United States:

Maine: Kittery Point, on hickory nuts, 1921, and Nov., 1923, *Thaxter* (F).

Massachusetts: Canton, on oak twigs, *Linder, 1042* (L), chestnut bark, *Linder, 1014* (L); Cambridge, Fresh Pond, June 1, 1905, *R. Thaxter* (F); Stony Brook, May 30, 1892, *R. Thaxter* (F).

Connecticut: Franklin, May 18, 1899, *W. A. Setchell* (F).

Ohio: Canton, on *Quercus*, *A. P. Morgan* (F); Preston, *Morgan*, as *H. olivaceum.*

Missouri: Gray Summit, *Linder* (F, L, MBG 66538); Meramec Highlands, *Linder* (F, L, MBG 66514); Sulphur Springs, *Linder* (F, L, MBG 66480).

Iowa: Iowa City, on acorn, March 4, 1927, *G. W. Martin* (Ia).

British Guiana: Botanic Garden, Georgetown, *Linder, 234A* (F, MBG 66595).

2. Helicosporium aureum (Corda) Linder, n. comb.

Helicomyces aureus Corda, Icones Fung. **1**: 9. *pl. 2, fig. 142.* 1837.

Helicosporium pilosum Ell & Ev. Torr. Bot. Club Bull. **24**: 476. 1877.

Plate 14, figs. 1–8; plate 30, fig. 3.

Forming a "Wax Yellow" to "Dull Citrine" or "Olive Citrine," loose cottony layer that is separable from the substratum. The conidiophores simple, erect, stiff and bristle-like at first, later branching from near the apex almost at right angles to the main rhachis, deep fuscous below, lighter above, with subhyaline tips that are easily broken off, 390–650 μ × 5.4–7.2 μ below, tapering upwards to 2 μ. Conidia pleurogenous, on hyaline, bladder-like projections, 5.4 × 5.4–10 μ, produced laterally on the lower parts of the conidiophores, dilute yellow, "Wax Yellow" in mass, the filament indistinctly 12–20-times septate, 3-times coiled, 1–2 μ in diameter; diameter of the coiled conidium 16–19 μ.

This species, microscopically, is quite distinct from other members of this genus, the outstanding characters being the erect seta-like conidiophore which at maturity branches above almost at right angles to the main axis, and the bladder-like projections on the lower part of the conidiophore. No types of this species exist, so far as the writer is aware, although we have Corda's figures as a basis for determination. In these figures the helical spores are shown spirally arranged around the conidiophore which Corda thought to be the host for the parasitic spores. The conidia are shown with flaring bases which appear to be a portion of the

bladder-like projections. Since Corda was acquainted with *Helicosporium vegetum*, it seems improbable that there was confusion between these in his mind, nor is there evidence that *Helicosporium gracile* entered into his consideration. Hence there seems to be little doubt but that this species is the one he described.

Specimens examined:

Exsiccati: Ell. & Ev., Fungi Columb., 1361; N. Am. Fungi, 125, as *H. vegetum.*

United States:

Maine: Kittery Point, Sept. 26, 1892, with *Helicoon ellipticum*, *R. Thaxter* (F).

Massachusetts: Canton, *Linder, 253, 1036* (L); Sharon, Oct. 15, 1918, *Piguet*, as *Helicosporium vegetum* (F); Readville, Oct. 1896, *R. Thaxter* (F).

New Jersey: *J. B. Ellis, 1434*, as *H. olivaceum* var. *canum* Ellis, in herb. (NY).

Connecticut: Milford, May, 1891, *R. Thaxter* (F).

South Carolina: *Ravenel* (K).

Florida: Eustis, September, October, 1897, *R. Thaxter* (F).

Alabama: Montgomery, *Burke* (MBG 51247a).

Mississippi: Starkville, Apr. 3, 1899, *G. W. Herrick* (F).

Iowa: W. Okaboji, July, 1928, *G. W. Martin* (MBG 65285, and Ia).

Louisiana: March, 1896, *Langlois, 2453*, type of *Helicosporium pilosum* (F).

3. **Helicosporium guianensis** Linder, n. sp.

Plate 13, figs. 5–6.

Colonies effuse, short-cottony, "Oil Yellow." The conidiophores at first simple and erect, later becoming bent, not branching above, somewhat loosely branched below and occasionally anastomosing, up to 480 μ long, 3.6–4.5 μ in diameter below, slightly tapering upwards to a rounded point. Conidia borne pleurogenously, at first on minute hyaline teeth, later on bladder-like projections which may continue growth, enlarge and become somewhat sympodially branched and dilute fuscous, yellow in

mass, hygroscopic, 3–3½-times coiled when tightly wound, the coil then 21.6 μ in diameter, larger when uncoiled, the filament 1.4–1.6 μ in diameter.

On buried twigs. South America.

This species resembles *Helicosporium vegetum* but differs from that species by the sympodially branched, subhyaline spore-bearing projections which arise from the lower part of the mature conidiophores. However, it more closely resembles *H. aureum*, from which it differs by the more slender conidiophores, the fact that the conidiophores do not branch above, and by the characters of the bladder-like projections.

Specimen examined:
British Guiana: Georgetown, Oct. 4, 1923, *Linder*, TYPE (F).

4. **Helicosporium gracile** (Morgan) Linder, n. comb.
Helicomyces gracilis Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 40. *fig. 2.* 1892.

Plate 13, figs. 4, 7; plate 14, figs. 9–11.

Mycelium effuse, forming an arachnoid, "Oil Yellow" to "Yellowish Citrine" colony. Conidiophores creeping and giving rise to erect, simple or branched, dilute fuscous or dilute olivaceous branches up to 150 μ long, 2.5–5 μ thick. Conidia hyaline or yellow in mass, borne singly on minute, hyaline, cylindrical teeth on the creeping fertile mycelium or on the lower portions of the erect conidiophores, filiform, multi-guttulate or indistinctly multi-septate, the filament coiled 3–3¼ times, 70–90 μ in length (Morgan), 1–1.5 μ thick; diameter of the coil 10–15 μ.

On dead bark of Sassafras (Morgan) and on decaying twigs and acorns of *Quercus*.

In gross appearance this species resembles *Helicosporium aureum* and *H. vegetum*. Microscopically it is distinguished from both by the creeping habit and the pellucid dilute fuscous or dilute olivaceous color of the mycelium.

Specimens examined:
United States:
Massachusetts: Canton, *Linder* (L).
Ohio: Preston ?, *A. P. Morgan*, TYPE (Ia).
Iowa: Iowa City, on acorn, March 4, 1927, *G. W. Martin* (Ia).

5. **Helicosporium lumbricoides** Saccardo emend. Matruchot, Recherches sur le développement de quelques Mucédinées, pp. 5–37. *pl. 1–2.* 1892.

Helicosporium lumbricoides Saccardo, Michelia **1**: 86. 1874.

Helicosporium griseum Berk. & Curt. Grevillea **3**: 51. 1874.

Helicosporium cinereum Peck, N. Y. State Bot. Rept. **33**: 28. *pl. 2, figs. 4–6.* 1880.

Helicosporium leptosporum Saccardo, Syll. Fung. **4**: 559. 1886.

Helicomyces cinereus (Pk.) Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 41. *fig. 3.* 1892.

Plate 15, fig. 5; plate 31, fig. 7.

Colony effuse or in small patches, pinkish-gray, light gray, or brownish, cottony, easily separable from the substratum. Conidiophores upright or ascending, much-branched and frequently anastomosing to form a network, subhyaline to deep fuscous, 3.6–4.4–(6.3) μ in diameter, forming a loose layer of hyphae up to 400 μ thick. Conidia pleurogenous, borne singly on delicate hyaline teeth on the lower three-fourths of the conidiophores, hyaline or white to pinkish in mass, the filaments hygroscopic, 0.9–2 μ in diameter, 3–4-times coiled, indistinctly many-septate; diameter of coiled conidia 18–25 μ or larger when somewhat uncoiled.

Growing on bark and decaying wood, mostly of deciduous trees. Wide-spread.

This species is a rather abundant one in the temperate regions. It is somewhat variable in its micro- and macroscopical appearance. The colony is regularly cottony and separable from the substratum. In color it is generally light gray or olivaceous but occasionally is dilute pink because of the spores and also may vary with that of the conidiophores. Rapidly growing or young conidiophores are frequently subhyaline, even to the base, but these with age become deep fuscous. Just as the color varies with the condition of the fungus, so does the frequency of anastomosis of the branches, but the plant is always essentially the

same, so that splitting off of species or even varieties seems highly unprofitable.

The type specimen of *H. griseum* B. & C., in Kew Herbarium, and the co-type of *H. cinereum* Pk. agree in all respects. *Helicosporium leptosporum* of Saccardo was published to care for *H. griseum* B. & C., since that name was preëmpted by *Helicoma griseum* Bonorden which was transferred to the genus *Helicosporium* by Saccardo. The writer has been unable to study the type of *H. lumbricoides* of Saccardo, who in publishing the species stated that the spore filaments were 4 μ in diameter. None of the specimens under this name in European or American herbaria possess spores with filaments of such a diameter. It seems advisable, therefore, from lack of evidence to the contrary, to accept Matruchot's emendation.

Specimens examined:

Exsiccati: Ell. & Ev., N. Am. Fungi, 2nd series, 2598; Ell. & Ev., Fungi Columb., 90.

Germany: Dauerbachgrab, Purkersdorf, June 5, 1904, *von Höhnel* (F).

Belgium: *Bonnier, 1* (K).

United States:

Maine: Kittery Point, on oak bark, July 26, 1922, Aug. 12, 1922, *Thaxter* (F); on red-oak bark, July 30, 1921, *Thaxter* (F); Cutts Isl., on oak bark, Aug. 1, 1922, and Aug. 12, 1922, *Thaxter* (F).

Massachusetts: Waverley, on *Ulmus*, Oct. 1899, on *Platanus*, Oct. 1892, on wet boards, Oct. 4, 1892, *Thaxter* (F); Canton, on chestnut bark, *Linder, 1917*, on decaying wood of *Fraxinus*, *Linder, 1349*, (L); Sharon, on oak plank, *Piguet* (L); Cambridge, Fresh Pond, June, 1895, *Thaxter* (F).

Connecticut: New Haven, on wood, in greenhouse, *Thaxter* (F), on rattan in greenhouse, 1890, *Thaxter* (F).

New York: North Greenbush, June, *Peck*, type of *Helicosporium cinereum* (NY and probably NYS); Milford, May, 1891, *Thaxter* (F).

New Jersey: Newfield, on old corn stalks, May, 1893, *Ellis*, in Ell. & Ev., Fungi Columb. 90.

South Carolina: *Ravenel*, type of *Helicosporium griseum* B. & C., in herb. Berkeley, 2446 (BM).

Louisiana: *Langlois, 675* (NY).
Missouri: Gray Summit, *Linder* (MBG 66570).
Ohio: Preston, on bark of *Platanus, Morgan,* in Ell. & Ev., N. Am. Fungi.
Iowa: Iowa City, on old cup of acorn, *G. W. Martin* (Ia).

6. Helicosporium lumbricopsis Linder, n. sp.

Plate 16, fig. 6; plate 17, figs. 5–6.

Colonies effuse, "Dark Olive" or "Pallid Neutral Gray" from numerous spores, occasionally with a slight pink tinge. Conidiophores at first simple, erect, from fuscous, repent mycelium, later branching, bending, and anastomosing, under high power of the microscope "Dresden Brown" to "Buckthorn Brown," the terminal cells of the branches hyaline, 25–200 × 3.6–5.4 μ, tapering upwards, bearing conidia acrogenously or pleurogenously on short hyaline teeth. Conidia hyaline, hygroscopic, the filament 3–4-times coiled, 1.8–2.5 μ in diameter, 18–23-times indistinctly septate, diameter of the coiled spore 21–28 μ.

On decaying wood. Tropical or subtropical.

Microscopically this species in its mature condition somewhat resembles *Helicosporium lumbricoides*, but differs from that species in the thicker conidial filaments, the greater diameter of the coiled spores, and the more robust conidiophores. Macroscopically the two species are distinct in that *H. lumbricopsis* does not form a loose, cottony, pulvinate colony that is easily separable from the substratum.

Specimens examined:
United States:
Florida: Cocoanut Grove, January, 1898, *Thaxter,* TYPE (F).
Venezuela: *Blakeslee* (F).
British Guiana: Georgetown, on buried twigs, *Linder, 277* (L); Bartica, *Linder, 727* (F).

7. Helicosporium decumbens Linder, n. sp.

Plate 15, figs. 1–2.

Colony effuse, stiff-velvety, dark brown or "Sepia." Conidiophores at first erect, simple, later branched, decumbent, fuscous

below, dilute fuscous towards the apices, 75–200 × 4–5 μ. Conidia pleurogenous, at first on minute hyaline teeth, later on bladder-like projections which subsequently elongate to become short branches, hyaline, filaments 1–2-times coiled, .75–1.5 μ thick, coil 6–9 μ in diameter.

On *Carpinus*. Austria.

This species is a characteristic one distinguished from all others in the small size of the spore and the few coils; also by the characteristic type of branching and swellings of the conidiophores.

Specimen examined:

Austria: Steinbachgrabe, Wienerwald, *von Höhnel, 2664*, TYPE (F).

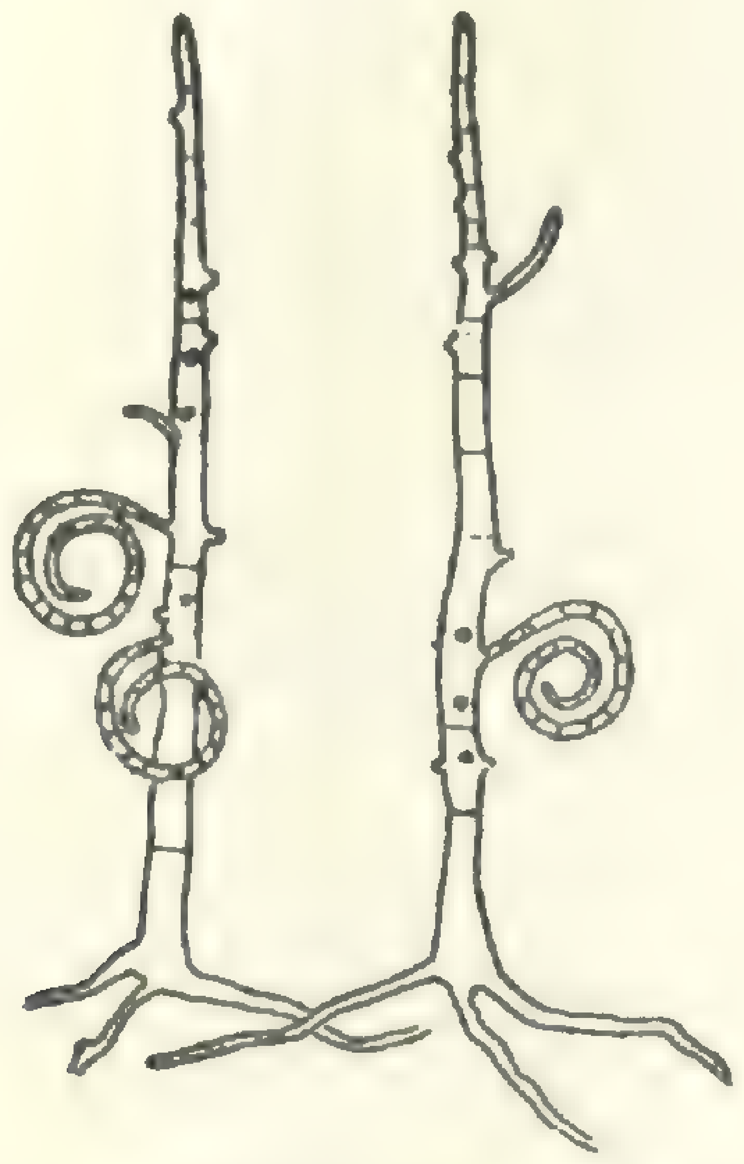


Fig. 6. *H. griseum.* After Bonorden.

8. **Helicosporium griseum** (Bon.) Saccardo, Syll. Fung. **4**: 559. 1886.

Helicoma griseum Bonorden, Handbook, p. 74. *fig. 77.* 1851.

Plate 15, figs. 3–4.

Colony effuse, cottony, gray. Sterile mycelium dilute fuscous, septate, repent, often occasionally ascending and then tending to become fasciculate. Conidiophores erect or bent, simple or rarely branched, occasionally creeping and branched, dilute fuscous, becoming hyaline above, conspicuously septate, 108–250 × 3.6–4.5 μ, tapering above to slender apex 1–1.8 μ in diameter.

Conidia pleurogenous, borne singly on slender (1 μ) hyaline teeth, hyaline, the filaments 2½–4-times coiled, indistinctly many-septate, 1 μ in diameter; diameter of coiled spore 12.6–14.4 μ.

On decaying wood. Europe.

This appears to be very close to *Helicosporium albidum* and *Helicosporium phragmites*, but differs in the smaller diameter of the spore filaments and in being less frequently branched.

No spore measurements have been given, either by Bonorden or Saccardo, although Saccardo states that the conidia are 15–20-septate. The above description is drawn from a specimen in the von Höhnel collection which was classified as this species, and which agrees closely with the figure published in Bonorden's 'Handbook.'

Specimen examined:

Austria: Purkersdorf, Wienerwald, June 1, 1902, *von Höhnel* (F).

9. **Helicosporium pallidum** Cesati, in Rabenhorst, Bot. Zeit. **13**: 598. 1855.

Plate 16, fig. 1.

Colonies tufted, gray, becoming pinkish. Conidiophores sparsely branched below, simple above and occasionally anastomosing, dilute fuscous to subhyaline, hyaline above, slightly tapering upwards; septa inconspicuous, up to 580 μ long, 1.5–4 μ thick. Conidia borne pleurogenously on slender cylindrical teeth, hyaline, the filaments 1 μ in diameter, coiled 2–3½ times; diameter of coiled spore 10–15 μ.

On decaying wood. Europe.

There is a great similarity between this species and the preceding, the only difference being that in this one the septa of the conidiophores are rather inconspicuous and the conidiophores are more elongate and slender and anastomose above with neighboring ones. It is quite possible that the two species are identical and are based on differences which depend on the age of the organism.

Specimen examined:

Exsiccati: Rabenhorst, Herb. Myc., ed. 2, 62, TYPE.

Italy: Vercelli, in Rabenhorst, Herb. Myc.

10. **Helicosporium albidum** Grove, Jour. Bot. **24** (N. S. **15**): 204. *pl. 267, fig. 6.* 1886.

Hyphae erect, septate, hyaline, at first simple, then branched below, 2½–3 × 200–300 μ, branches long, ascending, sterile, and flagelliform; conidia pleurogenous, substipitate, hyaline, multiguttulate, 2–2½ μ diameter (of conidial filament), base attenuate, apex rounded, densely 4 times convolute, diameter of coiled spore 15–20 μ. Colonies white, velvety.

On slender branches of *Rubus fruticosus*, Middleton, April. *Grove.*

11. **Helicosporium phragmites** von Höhnel, Ann. Myc. **3**: 338. 1905.

Plate 16, figs. 2–5.

Colonies effuse, cottony, brownish-gray, tinged pink by spores. Conidiophores branched below, simple above, very dilute fuscous below, hyaline above, up to 350 μ long, 2.5–4.5 μ in diameter, slightly tapering upwards to bluntly rounded apices, bearing spores pleurogenously on slender hyaline teeth, 1 × 1–2.5 μ. Conidia hyaline, light pink in mass, the filament 3–4-times coiled, multiseptate, 1.5–2 μ in diameter, coiled spore 15–18 μ in diameter.

This species, except for the slightly smaller spores, appears to be identical with *Helicosporium albidum*, but since the writer has been unable to see a representative of the latter species and also since von Höhnel has described the perfect stage of the former, it seems advisable, for the present at least, to maintain the two as distinct. Von Höhnel, in his description, stated that the perfect and imperfect stages were in association. Study of the type material indicates clearly that the two stages are not only in association, but are actually connected. The description of the perfect stage follows:

Acanthostigmella genuflexa von Höhnel, Ann. Myc. **3**: 327–328. 1905.

Perithecia superficial, scattered, spherical or subovoid, 70–80 × 100 μ, the perithecial walls thin, brown, ornamented around the short cylindrical ostiole with dark brown, recurved, septate

bristles 60–80 × 4–5 μ, otherwise the perithecium is smooth. Paraphyses lacking; asci broadest in the middle, tapering towards either end, 30–35 × 8 μ; spores as many as 8, irregularly arranged, greenish-hyaline or dilute olive in mass, spindle-shaped, tapering towards the bluntly rounded ends, 1–2-times septate.

Specimens examined:

Austria: Tullu, on decaying stalks of *Phragmites communis*, June 3, 1905, *von Höhnel*, TYPE (F).

United States:

Maine: Kittery, on old *Carex* in bottom of dried-up pond, June, 1893, *Thaxter* (F).

12. Helicosporium serpentinum Linder, n. sp.

Plate 17, figs. 1–4.

Colony effuse, hirsute, "Saccardo's Olive" to "Saccardo's Umber." Conidiophores light brown, becoming subhyaline in terminal cells, at first simple, erect, from creeping hyphae, then bent and occasionally branched, rather closely septate, the length of the cells being 1½–3 times the width, 76–216 × 5.4–9 μ. Conidia produced acro-pleurogenously on hyaline, simple or branched sporogenous teeth, 2–4 μ in diameter, "Cream buff" to "Chamois" under the high power of the microscope, hygroscopic, the filament 15–30-septate, breaking readily at the thicker septa where the filament is slightly constricted, 8.5–11 μ thick in the middle, tapering to 5.4–4.6 μ at the rounded distal end, 4.5 μ at the truncate basal end; conidia when coiled 55–100 μ.

On decaying wood. Missouri.

This species is closest to *Helicosporium nematosporum* but differs from that species by the dimensions of the spores and conidiophores and the stouter and branched sporogenous teeth.

Specimen examined:

United States:

Missouri: Pacific, on decaying wood, Oct. 1927, *Linder*, TYPE (F, L, MBG 64721).

13. Helicosporium nematosporum Linder, n. nom.

Helicomyces fuscus Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 48. *fig. 14.* 1892.

Plate 18, figs. 1–5.

Effuse, forming a thin "Dresden Brown" hirsute colony. Sterile mycelium repent, septate-branched, light brown, translucent, giving rise to distant or subdistant concolorous conidiophores. Conidiophores simple or sparsely branched and occasionally anastomosing, erect or ascending, septate, brownish, translucent, hyaline at the terminal cells, 90–250 × 5.4–8.0 μ, tapering slightly towards the abruptly rounded apex. Conidia pleurogenous, borne singly on conspicuous hyaline teeth (1.8 × 1.8–3.6 μ), hygroscopic, dilute fuscous, even, 28–60-septate, 2½–4-times coiled, the filament 4.5–6 μ thick, gradually tapering to 3 μ at both extremities, the distal extremity bluntly rounded, the basal bluntly rounded and flattened obliquely where it is attached to the sporogenous teeth; diameter of spore when tightly coiled 45–50 μ, when loosely coiled 85–100 μ.

Growing on decaying wood.

In addition to the helical spore, there is present in the Connecticut material the "sclerote pedicelée" of Matruchot, which is shown in pl. 18, fig. 2. In the British Guiana specimen, the perfect stage has been found in connection with the imperfect one. In the tropical material, although the conidiophores are simple and erect at first, they show a strong tendency to anastomose in the more mature stages of development.

Specimens examined:

United States:

Connecticut: New Haven, in greenhouse on rattan, *Thaxter* (F).

Ohio: Preston, on wood of *Juglans*, *Morgan*, TYPE (F).

British Guiana: Georgetown, on sheath of royal palm, *Linder*, *236* (F, L); Plantation Vryheid, Demerara River, on sheath of manicole palm, *Linder*, *881* (F, L).

The description of the perfect stage is as follows:

Lasiosphaeria nematospora Linder, n. sp.

Perithecia scattered, black, subspherical with ostiole as a low papilla, at first with scattered bristles or a few conidiophores, later almost smooth, 200–300 μ in diameter. Asci clavate. Ascospores distichous or tristichous, hyaline at least before completely mature and then dilute fuscous, 5–11-septate, 45–58 × 3.1–3.6 μ, tapering toward both extremities, somewhat spirally twisted.

On sheath of royal palm, Botanic Garden, Georgetown, British Guiana, *Linder*, *236*, TYPE (F).

14. Helicosporium Elinorae Linder, n. sp.

Plate 18, figs. 6–10.

Colony effuse, bristly, "Raw Umber." Conidiophore erect or curved, ascending from repent mycelium, dilute "Buckthorn Brown" under the high power of the microscope, to fuscous, the terminal cells lighter, granulate-roughened by crystal-like deposits, 180–260 × 7.2–10.5 μ. Conidia pleurogenous on stout (4 × 5–7 μ) hyaline teeth, dilute fuscous to fuscous, hygroscopic, filament coiled 3–5 times, often in 3 planes, multiseptate, 6.3–8 μ in diameter, slightly tapering to the rounded distal end and to truncate basal end.

On decaying wood. Surinam.

This species, in addition to differences in dimensions, differs from the preceding species by the granular roughening of the terminal cells of the conidiophores. The perfect stage of this species was also found connected with the above-described imperfect stage, and is described as follows:

Lasiosphaeria Elinorae Linder, n. sp.

Perithecia subovate, scattered, black with brownish hairs among which are often conidiophores, 480 × 520 μ; asci 8-spored, clavate, 144 × 12.6–16.2 μ; paraphyses slender, 1–1.5 μ, wavy, hyaline, exceeding the length of the asci; ascospores dilute fuscous, the basal cell often conspicuously narrowed, hyaline, the distal cell bluntly rounded, 5–5.5 × 54–63 μ.

The writer takes great pleasure in dedicating this species to his wife, whose interest has ever been a source of encouragement.

Specimen examined:

Surinam: Upper Cottica River, on decaying chips of wood, *Linder, 382*, TYPE (F, L).

SPECIES IMPERFECTLY KNOWN

Helicosporium albo-carneum (Cr.) Saccardo, Syll. Fung. **4**: 559. 1886.

Helicotrichum albo-carneum Crouan, Florule Finistere, p. 12. 1867.

"Touffes de 2 à 3 millim., d'un blanc-carne, à filamente rampants emettent des filaments cloisonnés peu rameux supportant lateralment des sporanges heliciformes.

"Sur une tige mort de Ronce."

From the meager description above, it is apparent that this species should be placed in the genus *Helicomyces,* since the repent mycelium and the hyaline to pinkish spores definitely relate it to *Helicomyces roseus.*

Helicosporium brunneum Schulzer & Saccardo, Hedwigia **23**: 126. 1884.

Helicotrichum brunneum Schulzer, Flora **60**: 272. 1877.

"Effusum, tenue, brunneum, subvelutinum; hyphis primariis fasciculato-stipitiformibus subramosis (an propriis ?) hyphis fertilibus ex illis egredientibus, filiformibus non collabescentibus subsimplicibus, septulatis, melleo-fuligineis 2–6 micr. d.; conidiis pleurogenis filiformibus in spiras tres arcte convolutis, dense septatis, fuligineis, ubi convolutis diam. 20–22 micr.

"Hab. in fragmentis ligneis Salicis pr. Vinkovce."

The above description is that of Schulzer and Saccardo in Hedwigia. In the original description of *Helicotrichum brunneum* in Flora, Schulzer gives additional information. Thus the thickness of the colony is given as about 3 mm., formed of many thin united threads that with their branches make a loose tangled "hyphasma." In addition to the description of the hyphae, the spores are also described as hygroscopic. Thus there is little doubt that this species belongs to the genus *Helicosporium.* From the fact that the hyphae anastomose, there is a suggestion that the species should be considered as very close indeed to *H. lumbricoides.* As a matter of interest, Schulzer remarks that *H. brunneum* grew in association with *Lasiosphaeria botellospora* De Not.

Helicosporium Ellisii Cooke, Quekett Microsc. Soc. Jour. **4**: *pl. 26, fig. 24.* 1877; Sacc. Syll. Fung. **22**: 1436. 1913.

This species was only figured by Cooke and was not described until Saccardo, using Cooke's figure as a basis, gave the following description:

"Conidiophoris erectis, strictis, obsolete septatis, non constrictis, filiformibus, 500–600 × 4–5 μ, brunneis; conidiis (acrogenis) cylindricis, spiraliter convolutis, 4–5-septatis, non constrictis hyalinis, totis (convolutis) 22 μ latis, spicalis binisternis, 4–5 μ cr.

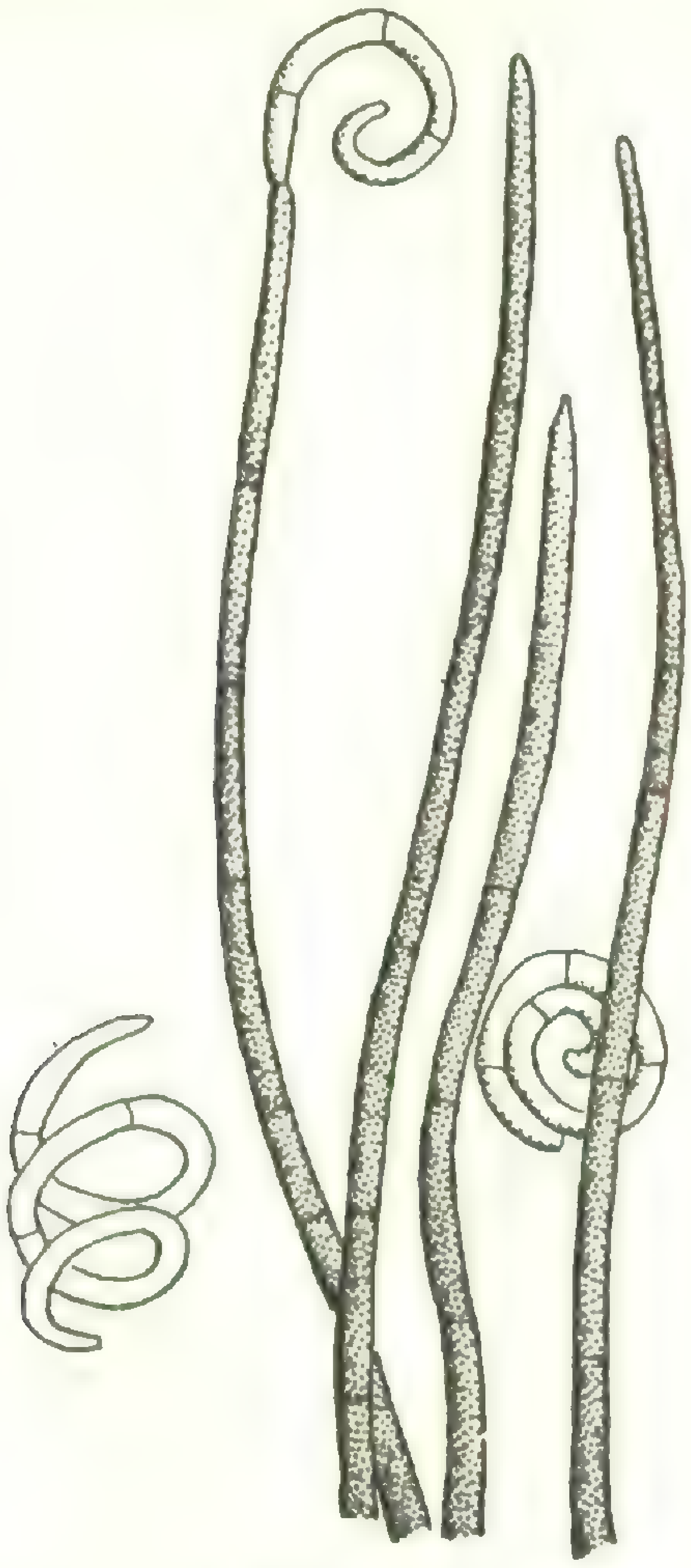


Fig. 7. *H. Ellisii.* After Cooke.

"Hab. ad truncos (?) in America boreali."

The validity of this species is very questionable since, figured on the same plate with it, is *H. vegetum*, the spores of which were shown as being produced acrogenously, not pleurogenously, as should be the case. Furthermore, the writer, in going over the collections in the British Museum and in the herbarium at Kew, was unable to find any material representing the species. Therefore, before accepting it as valid, it seems best to await the discovery of Cooke's type or at least material that is comparable.

Helicosporium herbarum Sacc., Bomm. & Rouss. in Bommer, E. & M. Rousseau, Soc. Roy. Bot. Belg. Bull. **29**: 299. 1891.

"Groupes petits, arrondis, floconneux, couchés, d'un gris cendré. Filaments rampants, hyalins puis fuligineux, longuement ramifiés, flexueux, septés, 4.5–5, émettant sur leur parcours, de trés courtes verrues hyalines sur lesquelles naissent des conidies nombreuses, 1.5–2, hyalines, filiformes, enroulées en une

spire serrée formant 4 tours, pluriseptées, ne se déroulant pas, mais se divisant. La conidie enroulée mesure 13–15 de diamètre. —Sur une tige morte d'*Epilobium hirsutum*. Groenendael. Oct. 1887.

"Espèce voisine d'*Helicosporium albidum* Grove, dont elle diffère par les filaments brunâtres, toujours couchés, les conidies sessiles, septées à base non atténuée, etc."

The writer has been unable to obtain material of this species. There are, however, few characters that could be considered of weight in separating it from *Helicosporium albidum*, *H. griseum*, *H. pallidum*, and *H. phragmites*, unless it is the size of the spores. *H. albidum* has thicker conidial filaments (2–2.5 μ), while those of *H. griseum* and *H. pallidum* are thinner (1 μ). There thus remains the possibility that *H. phragmites* is identical with this and should be considered a synonym, but until material of *Helicosporium herbarum* is available for comparative study, such a treatment, in view of the uncertainty concerning this group of five species, would be decidedly premature.

Helicosporium populi (Cr.) Saccardo, Syll. Fung. **4**: 560. 1886.
Helicotrichum populi Crouan, Florule Finistere, p. 12. 1867.

"Touffes arrondies de 1 à 2 millim; grisâtres, formées par des filaments nombreux, cloisonées, rameux, dichotomés terminés à leurs sommets par des sporanges heliciformes.

"Sur la partie de l'ecorce d'un Peuplier mort."

Helicosporium prasinum Preuss, Linnaea **24**: 111. 1851.

"Thallo bombacino prasino; floccis intricatis, septatis; sporis flocciformibus, apice lateribusque in cylindro spiraliter tortuosis diaphanis dilute prasinis.

"Habitat in asseribus semiputridis."

Saccardo[1] suggests that this species may be synonymous with *H. pulvinatum*.

Helicosporium pulvinatum (Nees) Persoon, Myc. Eur. **1**: 19. 1822.
Helicotrichum pulvinatum Nees, Acad. Leop. Nova Acta **9**: 246. *pl. 5, fig. 15.* 1818.

"Caespitulis late effusis sordide albido-lutescentibus, demum

[1] Saccardo, P. A. Sylloge Fungorum **15**: 156. 1901.

obscurioribus; hyphis filiformibus, ramosis vel chlorino-fuligineis, 3–4 μ diam.; conidiis in spiras 2½–3 convolutis, 2 μ diam. continuis plurinucleatis, hyalinis, 70–80 μ long."

The above description and figure is taken from Saccardo's[1] account of the species. If one may judge by the specimens under this name in the various exsiccati and in the herbaria of Europe

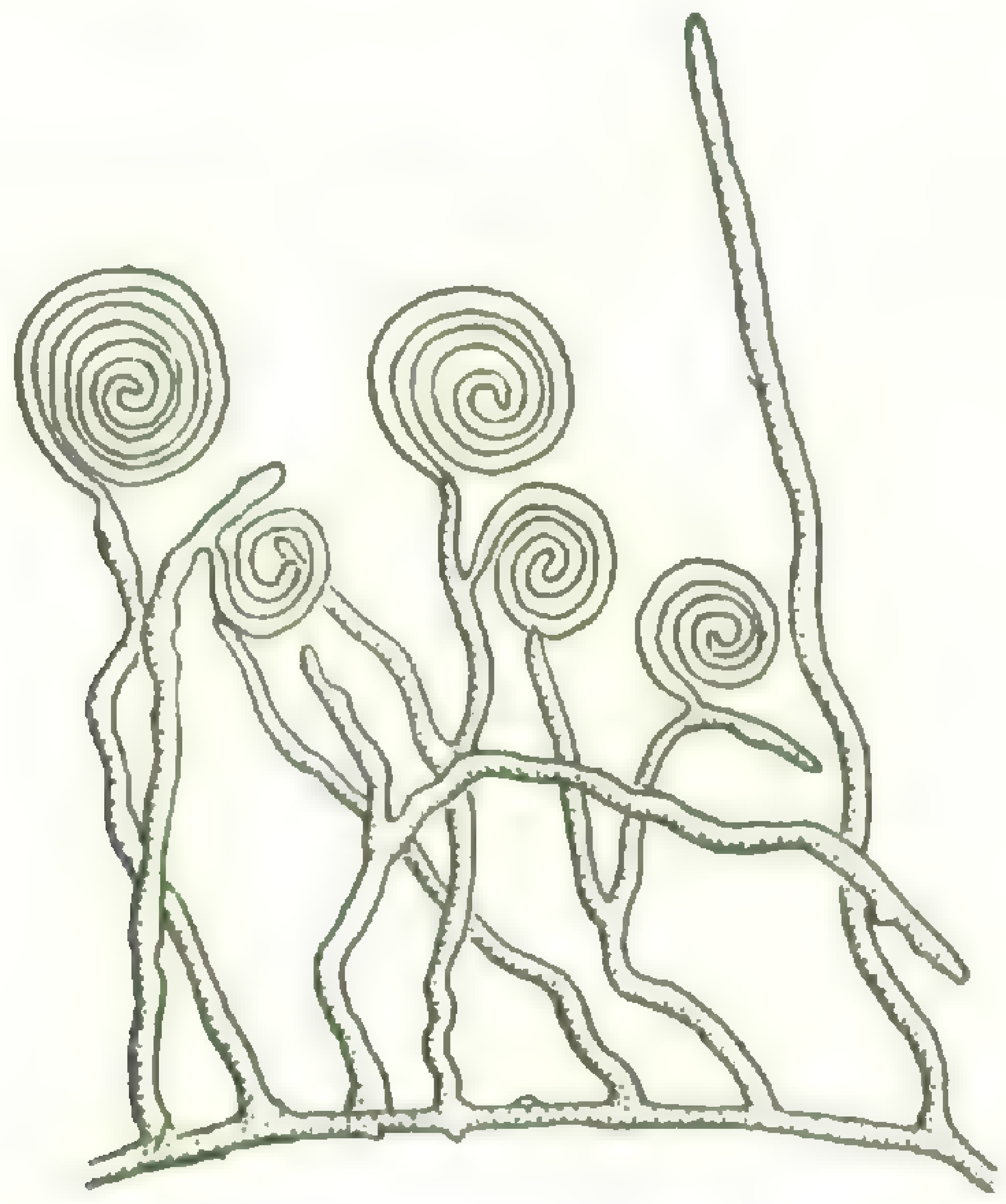


Fig. 8. *H. pulvinatum.* After Saccardo.

and America, this species should be considered as synonymous with *Helicosporium vegetum*, yet in view of the figure given by Saccardo, additional material must be studied before the status of the species can be determined. The writer has been unable to discover any specimens that correspond to the description given above.

EXCLUDED SPECIES

1. **Gyroceras nymphaearum** (Rand) Linder, n. comb.
   Helicosporium nymphaearum Rand, Jour. Agr. Res. 8: 219–232. *pl. 67–70.* 1917.

Mycelium intercellular, light brown, often hyaline in culture, septate and branched. Conidiophores slender, 2–3 μ in diameter, inflated at the apices, 6–7.5 μ, often becoming branched and thus producing several conidia in clusters. Conidia 60–170–(190) μ, brown, many-septate, strongly constricted at the septa, the apical cell subspherical or ovoid, flattened at the point of contact with

[1] Saccardo, P. A. Syll. Fung. 4: 557. 1886; Fungi Ital. *fig. 811.* 1881.

the penultimate cell; the basal cell rounded-tapering; the remaining cells generally longer than wide and minutely tuberculate.

Parasitic on leaves of *Nymphaea* sp. New York, New Jersey, and Washington, D. C.

This species differs from all known species of *Gyroceras* because of the minutely tuberculate sculpturings of the conidial walls, the deep constrictions at the septa, and the morphology of the conidiophores. Because of the absence of definite aerial conidiophores and on account of the structure of the spores, this species must be excluded from the genus *Helicosporium.*

Rand (*l.c.*) reports the presence of sclerotia that are rounded, subcarbonaceous, and measuring 150–190 μ in diameter. No perfect stage has as yet been associated with this species.

Specimen examined:

United States:

Washington, D. C.: *Rand,* TYPE (U. S. Dept. Agr. and slide F).

HELICOMA

Helicoma Corda, Icones Fungorum **1:** 15. *pl. 4, fig. 219.* 1837; Morgan, Cinci. Soc. Nat. Hist. Jour. **15:** 45. 1892.

Helicoryne Corda, Icones Fungorum **6:** 9. 1854.

Helicopsis Karsten, Rev. Myc. **11:** 96. 1889.

The type species is *Helicoma Mülleri* Corda.

Conidiophores various. Conidia hyaline, light-colored or fuscous, the filaments spirally coiled, stout in proportion to the length, not hygroscopic. Colonies effuse.

Since Corda originally described *Helicoma,* members properly belonging to the genus have been described, with few exceptions, in the genus *Helicosporium* following Saccardo's treatment. In view of the fact that members of this genus form a more or less homogeneous group of organisms characterized by the thickness of the spore filaments and their non-hygroscopic nature, the writer is following Morgan in restoring the genus to its original status. *Helicoryne* as originally described is obviously synonymous with *Helicoma;* in fact, the type species, *Helicoryne viride,* is a synonym of *Helicoma Mülleri.*

KEY TO THE SPECIES OF HELICOMA

1. Conidial coil 51–72 μ in diameter; filament 28–31 μ in diameter, 6–9-septate. .... *1. H. roseolum*
1. Conidia smaller 2

2. Coil of conidia 4–7 μ in diameter, filament 1 μ in diameter, hyaline.... .... *2. H. minutissimum*
2. Conidia larger........ 3
3. Conidiophore less than 60 μ long in mature plant........ 4
3. Conidiophore of mature plant more than 60 μ long........ 8
4. Conidium 7–10 μ in diameter, ¾–1½-times coiled, 1–3-septate, hyaline, on Sphaeropsidae........ *3. H. stigmateum*
4. Conidium larger, or at least colored, more frequently septate and coiled.... 5
5. Diameter of conidial filament 2–2½ μ; of coil 11–12.5 μ; conidia 12–20-times septate........ *4. H. microscopicum*
5. Diameter of conidial filament larger........ 6
6. Conidia tapering to the narrow or truncate basal ends........ 7
6. Conidia abruptly rounded at basal end........ 8
7. Conidia coiled 1½–1¾ times, the filament 4.5–5 μ thick, tapering to 1–1.5 μ at base, 8–10–(15)-times septate........ *5. H. polysporum*
7. Conidia coiled 2–3 times, 18–21 μ in diameter, multi-guttulate..... *6. H. repens*
8. Conidia 20–25 μ in diameter, 2–3-times coiled........ *7. H. limpidum*
8. Conidia 11–19 μ in diameter........ 9
9. Conidia 14.4–19 μ in diameter, 2-times coiled........ *8. H. monilipes*
9. Conidia 11–15.5 μ in diameter, 1½–1¾-times coiled........ *9. H. olivaceum*
10. Conidia 2–3-times coiled, 16–30-times septate........ 11
10. Conidia coiled fewer times........ 13
11. Conidia 36–44 μ in diameter, fuscous, septa deep fuscous.. *10. H. perelegans*
11. Conidia smaller, septa hyaline........ 12
12. Conidia on stout teeth, 2–3 μ in diameter, conidial filament 4–5.4 μ thick .... *11. H. violaceum*
12. Conidia on slender teeth, 1.2–2 μ in diameter, and obliquely attached.... .... *12. H. Morgani*
13. Conidia constricted at the septa, tightly coiled 1½–2 times, fuscous...... 14
13. Conidia not constricted at the septa........ 17
14. Conidia less than 30 μ in diameter........ 15
14. Conidia more than 30 μ in diameter........ 16
15. Diameter of conidial filament 4.5–5.4 μ........ *13. H. phaeosporium*
15. Diameter of conidial filament 5.4–8 μ........ *14. H. velutinum*
16. Diameter of conidia 30–35 μ, filament 8 μ........ *15. H. intermedium*
16. Diameter of conidia 36–40 μ, filament 11–12 μ........ *16. H. palmigenum*
17. Conidia more than 14.5 μ in diameter, if less then more than 4-septate.... 18
17. Conidia less than 14.5 μ, 4 or fewer septa........ 25
18. Conidia 30–35 μ, fuscous, with 10–16 dark septa........ *17. H. atroseptatum*
18. Conidia smaller, mostly fewer-septate........ 19
19. Conidia with truncate base, borne on stout (1.5–5 μ in diameter) teeth...... 20
19. Base of conidia tapering to an apiculate or tapering rounded end, sporogenous teeth less than 1.5 μ in diameter........ 21
20. Sporogenous teeth 1.5–2.5 μ in diameter, seldom more than once-branched; diameter of conidia 14–19 μ........ *18. H. Mülleri*
20. Sporogenous teeth 2–5 μ in diameter, at maturity more than once-branched; diameter of conidia 17–24 μ; "sclerote pedicelée" present.. *19. H. proliferens*
21. Conidiophores ascending or repent, much branched; base of conidia abruptly rounded and attached obliquely to the conidiophore...... *20. H. ambiens*

21. Conidiophores erect or bent, sparsely branched, or if much branched then more than 6 μ in diameter, and spores not abruptly rounded at base....22
22. Conidiophores erect, conspicuously branched, 6–8 μ in diameter, enveloped in part with a rough sheath. Chile..................*21. H. asperothecum*
22. Conidiophores not as above..23
23. Conidiophores 5.5 μ in diameter, becoming arcuate, hyaline; conidia 12–18 μ in diameter, yellow in mass. Grenada............*22. H. conicodentatum*
23. Colonies some shade of brown, fuscous, or black; conidiophores more than 5 μ in diameter, erect, simple, or sparingly branched..................24
24. Diameter of conidial filament 6–8–(10) μ, of conidia 15–20 μ; conidiophores mostly simple, constricted and ascending-arcuate above, with scattered masses of a purplish-black secretion......................*23. H. recurvum*
24. Diameter of conidial filament 4.5–5.4–(7.5) μ; of conidia 14.4–18 μ; conidiophores simple, rarely branched, erect or slightly bent, without masses of secretions or ascending-arcuate terminal portions......*24. H. Curtisii*
25. Conidiophores 63–243 × 2.8–3.6 μ, without lateral projections; spores 3–5-septate, 12–14.5 μ in diameter......................*25. H. fasciculatum*
25. Conidiophores 27–100 × 3.3–4.5 μ, with blunt, irregularly rounded lateral projections; conidia 3–4-septate, 9–12 μ in diameter......*26. H. simplex*

1. **Helicoma roseolum** Thaxter, n. sp.

Plate 19, figs. 1–3.

Mycelium scanty and evanescent, hyaline, septate, creeping over upright conidiophores of *Acrothecium* sp., giving rise laterally to branches which occasionally anastomose, generally 21–28 × 4.5–5.4 μ. Conidia acro-pleurogenous on lateral branches of scandent mycelium, tightly coiled, 1¼–1½-times abruptly rounded at distal end, the basal end terminated by a small, slightly tapering cell 7–10 × 7–9 μ, 7–9-septate, not or only slightly constricted at the septa; diameter of conidia at widest point 51–72 μ, of filament 28.8–31 μ.

On rotting fronds of *Euterpe* palm on ground. Grenada.

This beautiful and strikingly characteristic species, collected by Dr. Thaxter, was labelled in his herbarium as *Helicosporium roseolum*, which specific name the writer has adopted here.

In contrast to other members of the genus, the tooth-like projections do not bear the spores, but instead represent the isthmus inserted into the small basal cell of the spore.

Specimen examined:

Grenada, B. W. I.: Grand Etang, *Thaxter, 9*, TYPE (F).

2. Helicoma minutissimum Linder, n. sp.

Plate 19, figs. 4–8.

Colony appearing as inconspicuous whitish pulverulence on the substratum. Conidiophores hyaline, erect, simple or rarely branched, inconspicuously septate, 1–1.5 × 11–15 μ, bearing spores acro-pleurogenously; conidia hyaline, 1–1½-times coiled, 1–3-septate, the distal end bluntly rounded, tapering slightly towards the truncate basal end; diameter of conidial filament .75–1 μ; of coiled spore 4–7 μ.

On decaying elm bark. Massachusetts.

This species need not be confused with any other thus far described since its small size is thoroughly characteristic.

Specimen examined:

United States:

Massachusetts: Waverley, Oct. 14, 1909, *Thaxter*, TYPE (F).

3. Helicoma stigmateum (Reiss) Linder, n. comb.

Lituaria stigmatea Reiss, Bot. Zeit. **11**: 136. *pl. 3, figs. 1–10.* 1853.

Helicomyces niveus Bres. & Jaap, in Jaap, Verh. Bot. Ver. Prov. Brandenb. **58**: 43. 1916.

Helicomyces sphaeropsidis A. Potebnia, Gribnie symbionti. II. Sphaeropsidis i Helicomyces, 21–28, see p. 28. Kharkov, Moscovsk: M. Sergieu i K. Galchenk. 1912.

Plate 19, figs. 9–10.

Colonies minute, white, tufted, confined to region around ostiole of the sphaeropsidaceous substratum or host. Conidiophores either as upright teeth on the hyaline repent mycelium or as erect or bent, simple, hyaline branches 2–3 × 2–2.5 μ. Conidia hyaline, or white in mass, acrogenous, coiled ¾–1½ times, 1–3-septate, the filament 3–3.5 μ thick, tapering from the middle to the rounded base 1½–2 μ in diameter, the distal end bluntly rounded; the coiled spore 7–10 μ in diameter.

Parasitic or saprophytic on fruiting bodies of Sphaeriaceae or Sphaeropsidae.

The type of Reiss's species, *Lituaria stigmatea*, apparently is no longer in existence, from which fact there has been some doubt as to its identity. Von Höhnel[1] even went so far as to place this species in the tropical genus *Delortia*, the fruiting bodies of which are characterized by being gelatinous. If, however, Reiss's figures are compared with those of Potebnia, then the identity of the two species, *H. stigmateum* and *H. sphaeropsidis*, becomes quite evident, since they not only agree in appearance, but also in spore measurements. The fact that Reiss states that the spores are non-septate should not be considered too seriously as an objection since the septa, because of the small size of the spores and their refractive nature, would not be visible except under a high magnification or by the aid of stains. Further evidence of the identity is the similarity of habitat which Reiss states as "auf der Rinde eines dürren, feuchtliegenden Ulmenzweiges, welches von Sphärien bewohnt war." Jaap's material occurred on *Diplodia inquinans* and Potebnia's, otherwise admitted by him to be identical with Jaap's *H. niveus*, is stated to be parasitic on *Sphaeropsis pseudo-diplodia*.

Specimen examined:

Exsiccati: Jaap, O. Fungi Selecti Exsicc., 547.

Germany: Bergedorf, Schleswig-Holstein, *Jaap*, type of *Helicomyces niveus*.

4. **Helicoma microscopicum** (Ellis) Linder, n. comb.

Helicosporium microscopicum Ellis, Torr. Bot. Club Bull. **9**: 98. 1882.

Helicomyces microscopicus (Ellis) Pound & Clements, Minn. Bot. Stud. **9**: 659. 1896.

Plate 19, figs. 11–12.

Producing dense, minute, "Yellow Ochre" tufts. Conidiophores hyaline, erect or bent, up to 30 μ long by 2.7–3 μ in diameter. Conidia acrogenous or pleurogenous, on short hyaline teeth, subhyaline to yellowish, 12–20-times septate, closely 2–2¾-times coiled, the filament 2–2.5 μ in diameter; the coiled spore 11–12.5 μ in diameter.

[1] Von Höhnel, F. Kön. Akad. Wiss. Wien, math.-nat. Kl. Sitzungsber. **125**: 90. 1916.

On decaying catkins of *Alnus serrulata* on ground. New Jersey.

Specimen examined:

New Jersey: Newfield, *Ellis*, TYPE (NY, slide F).

5. **Helicoma polysporum** Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 46. *fig. 11.* 1892.

Helicosporium polysporum (Morgan) Saccardo, Syll. Fung. **11**: 639. 1895.

Plate 19, figs. 20–25.

Effused, forming a thin, whitish or light rose-colored stratum. Hyphae creeping, hyaline, much-branched. Conidiophores arising as erect or bent, hyaline, ramified branches from the repent sterile mycelium. Conidia hyaline, borne singly on hyaline teeth which may be either solitary or in pairs at the ends of the conidiophores or short branches of the conidiophores, occasionally single and pleurogenous, 8–15-times septate, 1½–1¾-times coiled, the filaments 4.5–5.4 μ thick, gradually tapering from the middle of the first coil towards the slender base, the terminal cell abruptly rounded; diameter of the coiled spore 16–19.8 μ.

On decaying bark. Ohio.

This species differs from all others in this group characterized by having short conidiophores, in that the conidia are broadest towards the distal end, tapering from near the middle of the spore to the very slender (1–1.3 μ in diameter) basal end, thus giving the spore its characteristic appearance.

Specimen examined:

United States:

Ohio: Preston, on inner bark of *Acer saccharinum*, *Morgan*, CO-TYPE (F).

6. **Helicoma repens** Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 47. *fig. 12.* 1892.

Helicosporium repens (Morg.) Saccardo, Syll. Fung. **11**: 639. 1895.

"Effused, forming a minutely flocculose, pinkish stratum. Hyphae creeping, septate, hyaline, with very short ascending branches, which are covered by the abundant spores. Spores hyaline, multiguttulate, coiled nearly 2½ times; the coil 18–21

mic. in diameter; the thread 80–100 mic. in length, about 4 mic. thick; the inner extremity obtuse, the outer (basal) long and tapering.

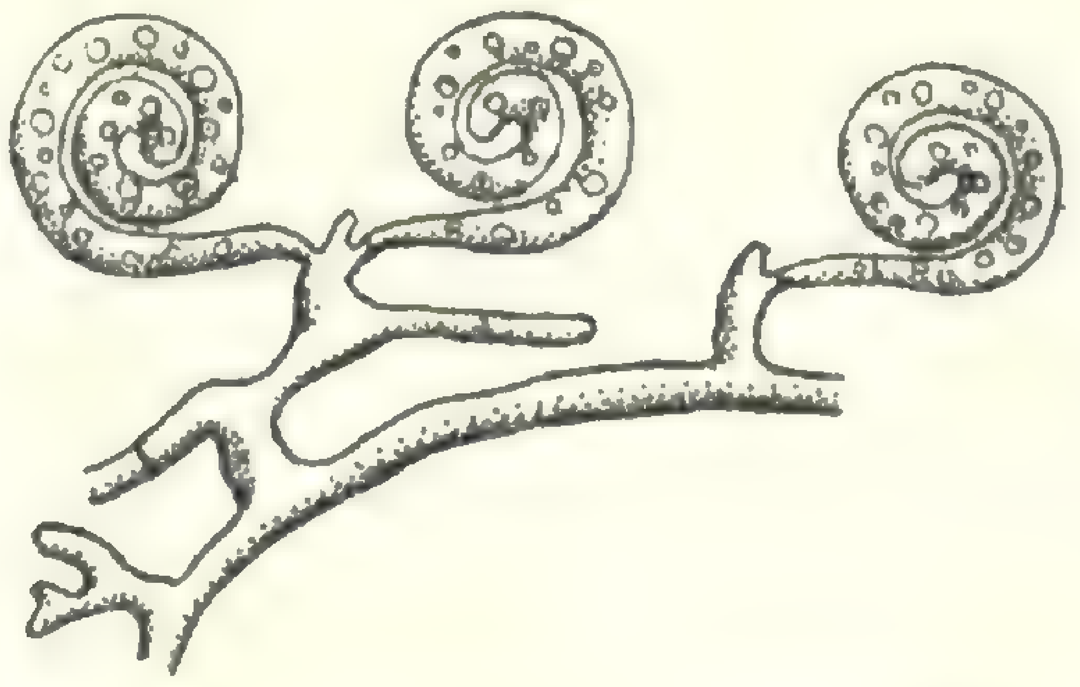


Fig. 9. *H. repens.* After Morgan.

"Growing on the inner bark of *Acer saccharinum.* The hyphae are very fine and creep on or beneath the surface so closely as to be distinguished with difficulty; the colored stratum is formed entirely by the abundant spores. The guttulae sometimes give the spore the appearance of being faintly septate."

7. Helicoma limpidum Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 47. *fig. 13.* 1892.

Helicosporium limpidum (Morg.) Saccardo, Syll. Fung. **11**: 639. 1895.

"Effused, forming a minutely flocculose, pale stratum. Hyphae creeping, septate, brownish hyaline, the spores borne at the apex of short lateral branches. Spores hyaline, multiseptate (15–20);

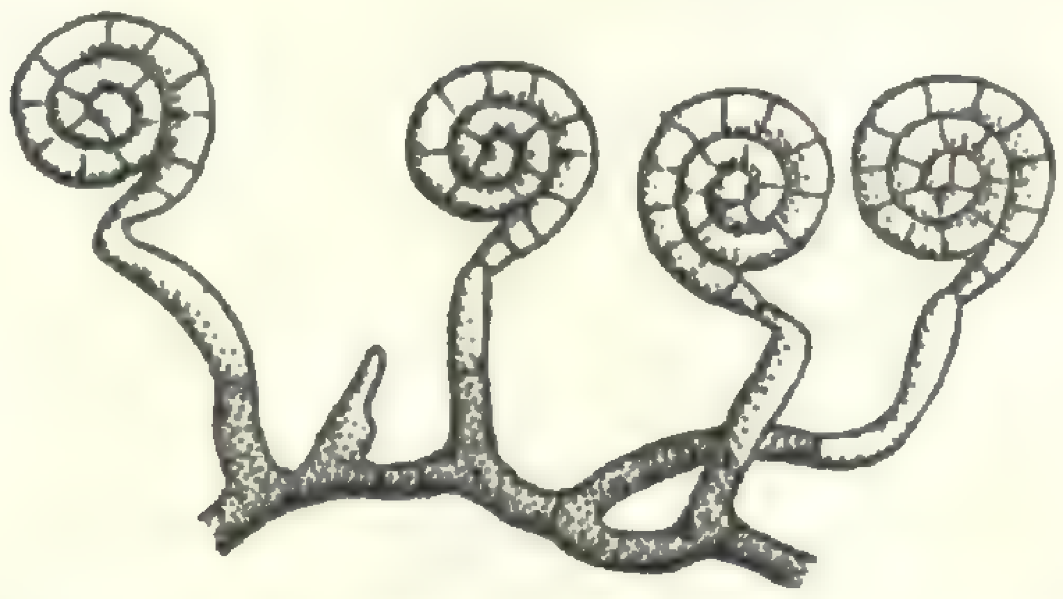


Fig. 10. *H. limpidum.* After Morgan.

the septa sometimes indistinct; coiled 2–3 times; the coil 20–25 mic. in diameter; the thread 80–110 mic. in length, about 4 mic. thick; the inner extremity acute, the outer obtuse.

"Growing on old wood of elm. The outer extremity of the spore does not taper, and is obtuse or sometimes truncate."

8. **Helicoma monilipes** Ellis & Johnson, in Ellis & Everhart, Proc. Acad. Nat. Sci. Phila. **1894**: 376. 1894.

Helicosporium monilipes (E. & J.) Saccardo, Syll. Fung. **11**: 639. 1895.

Plate 19, figs. 17–19.

Colonies appearing as brown, minute tufts less than 1 mm. in diameter. Conidiophores short, up to 55 μ long, 2–4 μ in diameter, subhyaline to dilute fuscous, septate, slightly to strongly constricted at the septa, erect, branched. Spores acrogenous, becoming pleurogenous by the elongation of the conidiophores, subhyaline to dilute fuscous, 2–2¼-times tightly coiled, (7)–10–15-times septate, dark brown, the filament 3.5–5 μ in diameter; the coiled conidium (12)–14.4–19 μ in diameter.

On bark of *Quercus*. Michigan.

Specimen examined:

United States:

Michigan: Ann Arbor, *L. N. Johnson*, Oct. 23, 1893, TYPE (NY and slide F).

9. **Helicoma olivaceum** (Karsten) Linder, n. comb.

Helicopsis olivaceus Karsten, Rev. Myc. **11**: 96. 1889.

Helicopsis punctata Peck, N. Y. State Mus. Bull. **167**: 26. 1912.

Plate 19, figs. 13–16.

Colonies brown, minute tufts less than 1 mm. in diameter. Conidiophores hyaline or dilute fuscous at the base, branched, 10–30 × 2–3 μ. Spores acrogenous, or pleurogenous by the elongation of the conidiophores, dilute fuscous, 1½–1¾-times tightly coiled, the septa black, 3–12; the filament slightly constricted at the septa, 3.6–5.4 μ thick, bluntly rounded at both ends; diameter of the coiled spore 11.7–15.5 μ.

On decaying wood and bark. Europe and America. Rare.

This species strongly resembles the preceding but differs from that in the smaller average size and the fewer turns of the conidia. The type of this species was kindly loaned to the writer by Dr. Harold Lindberg of the University of Helsingfors.

Specimens examined:

Finland: Surikaei, Nov. 1886, *Karsten*, TYPE (H, slide F, MBG).

United States:
New York: Lyndonville, *C. E. Fairman* (NYS, F).

10. Helicoma perelegans Thaxter, n. sp.

Plate 20, figs. 1–2.

Colonies small, .5–1 mm. in diameter, becoming larger by confluence, black. Conidiophores septate, dark brown with subhyaline terminal cells, branched subdichotomously or irregularly, arising singly or in clusters from the fuscous repent mycelium, 3.5–7 × 40–150 μ. Conidia acrogenous, rarely pleurogenous, fuscous except for subhyaline terminal cells, septa dark brown, 16–28; filament tightly coiled 2½–3 times, rarely once-coiled, 7.5–9 μ in diameter, tapering gradually towards the abruptly rounded or truncate basal end and the tapering, rounded distal end; diameter of coil 36–44 μ.

On bark of *Platanus*. Massachusetts. October.

The spores of this species closely resemble those of the Chilean *Helicoma atroseptatum*. The two species may readily be separated, however, by the difference in the size of the conidia and the branched conidiophores of this species.

Specimen examined:
United States:
Massachusetts: Waverley, *Thaxter*, as *Helicosporium perelegans* in herb., TYPE (F).

11. Helicoma violaceum Winter, in herb. n. sp.

Plate 20. figs. 3–5.

Colonies effuse, pulverulent-velvety, pinkish-gray. Conidiophores erect or ascending somewhat irregularly, simple or few-times branched, light fuscous, translucent, hyaline in terminal cells, 22–150 × 4.5–6.5 μ, arising from repent, fuscous sterile mycelium. Conidia hyaline, acro-pleurogenous, borne singly on short, stout, hyaline teeth 2–3.5 μ thick, coiled 2–3 times when mature, septa hyaline, conspicuous, 16–24; diameter of filament 4–5.4 μ, tapering slightly to abruptly rounded distal end and to truncate basal end.

On decaying wood. Germany.

Specimen examined:
Germany: *G. Winter*, TYPE (B, and slide F).

12. Helicoma Morgani Linder, n. nom.

Helicoma Berkeleyi Morgan, nec Curtis, Cinci. Soc. Nat. Hist. Jour. **15:** 48. *fig. 14.* 1892.

Plate 20, fig. 6.

Effused, forming a grayish-brown, loosely hirsute colony. Sterile hyphae creeping, translucent. Conidiophores erect or ascending, at first simple, then loosely and irregularly branching, brownish, translucent, terminal cells hyaline, 27–250 × 3.2–4.5–(5.4) μ. Conidia hyaline, becoming dilute fuscous with age, acropleurogenous, on short, slender teeth 1.2–2.5 μ thick, 18–30-times septate, the septa inconspicuous, 2–3-times coiled; filament 3.6–4.5–(5.4) μ; coil 21–27 μ in diameter.

On decaying wood. Ohio.

In Morgan's original description the diameter of the coiled conidia is given as 25–30 μ, and that of the conidial filament as 5–6 μ. The writer, studying material communicated to Dr. Thaxter by Morgan, found no spores to be over 27 μ in diameter; similarly, the diameter of the conidial filaments to be 3.6–4.5 μ, with an occasional filament measuring 5.4 μ.

Although resembling the preceding species, this one differs in its taller, more slender, and more loosely branched conidiophores; in its smaller conidia; the smaller sporogenous teeth; and by the fact that the conidia are mostly obliquely attached to the teeth.

Specimens examined:

United States:

Ohio: Preston, on rotting wood of *Juglans*, June 12, 1887, *A. P. Morgan*, TYPE (Ia; CO-TYPES F, NY); locality not given, May 12, 1887, May 6, 1888, June 3, 1888, June 28, 1888, Apr. 28, 1889, May 1, 1889, Jan. 1, 1890, Jan. 12, 1890, and Feb. 3, 1890, *A. P. Morgan* (Ia).

13. Helicoma phaeosporium Fresenius, Beitrage **3:** 99. *pl. 10–13, fig. 23–30.* 1863.

Helicosporium phaeosporium (Fres.) Saccardo, Syll. Fung. **4:** 561. 1886.

Helicosporium spectabile Fautrey & Lambotte, Rev. Myc. **17:** 70. *pl. 153, fig. 3.* 1895.

Helicosporium Boydii Smith & Ramsbottom, Brit. Myc. Soc. Trans. **5**: 168. 1915.

Plate 22, figs. 2–5.

Colony effuse, "Olive Brown," minutely hirsute. Conidiophores simple, erect, septate, subulate, fuscous except for hyaline terminal cells, 80–115 × 3–4.5 μ. Conidia acrogenous, rarely pleurogenous, soon deciduous, subhyaline to dilute fuscous, abruptly rounded at both ends, tightly coiled 1½–2 times, 8–12-times septate; filament 4.5–5.4 μ in diameter; diameter of the coiled spore 12.5–20 μ.

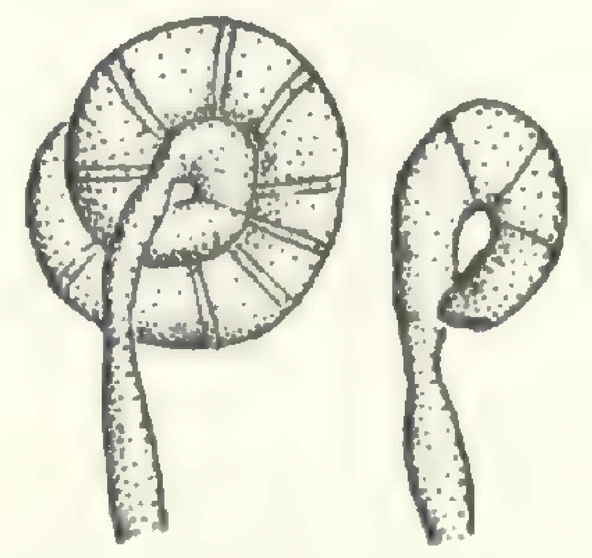


Fig. 11. *H. phaeosporium.* After Fresenius.

On decaying wood of coniferous or deciduous trees.

Specimens examined:

Exsiccati: Roumeguere, Fungi Select. Exsicc. 6737, type of *H. spectabile.*

England: West Kilbride, Ayreshire, *Boyd,* type of *Helicosporium Boydii* (BM, slide F).

Austria: *von Höhnel, 2660* (F).

United States:

Massachusetts: Canton, *Linder* (slide F, L).

14. Helicoma velutinum Ellis, Torr. Bot. Club Bull. **9**: 134. 1882.

Helicosporium velutinum (Ellis) Saccardo, Syll. Fung. **4**: 561. 1886.

Plate 22, fig. 1.

Colony effuse, minutely hirsute or velvety, "Olive Brown." Conidiophores erect, simple, septate, subulate, deep brown except for subhyaline terminal cells, 110–125 × 3.5–5.4 μ. Conidia acrogenous, soon deciduous, subhyaline to dilute fuscous, the terminal cells abruptly rounded; the filament more or less tightly coiled 1½–2 times, 10–14-times septate, slightly constricted at the septa, 5.4–8 μ thick; diameter of coiled conidia 18–25 μ.

On Magnolia. New Jersey.

This species, with the preceding and the two following ones,

forms a rather homogeneous group characterized by the simple erect conidiophores and the spores that are tightly coiled, rounded at both ends, and slightly constricted at the septa. They may be separated by their distinctive spore sizes.

Helicoma velutinum has been applied to *Xenosporella Berkeleyi* by Ellis and Morgan as a result of the former author's misdetermination of material sent to him from Louisiana by Langlois. The co-type of *Helicosporium velutinum* in the Farlow Herbarium, however, is the species above described.

Specimen examined:

United States:

New Jersey: Newfield, June, 1882, *Ellis*, CO-TYPE (F).

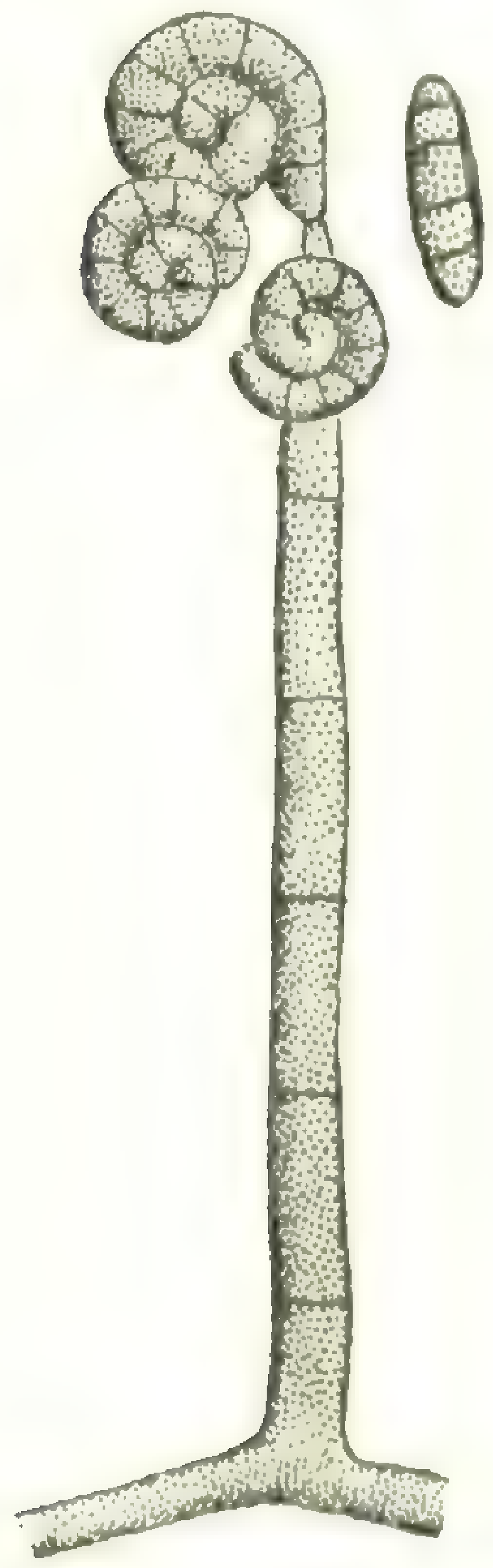


Fig. 12. *H. intermedium*. After Saccardo.

15. Helicoma intermedium (Penzig & Saccardo) Linder, n. comb.

Helicosporium intermedium Penzig & Saccardo, Icon. Fung. Javan. p. 105. *pl. 71, fig. 4*. 1904.

Colonies effuse, small or confluent, velvety, black. Conidiophores erect, rather stout, filiform, 130–160 × 7–8 μ, multiseptate, fuliginous, pallid above. Conidia acrogenous, dilute fuliginous, the filament coiled 2 times, 14–16-times septate, not constricted, 8 μ thick; diameter of the coiled conidia 30–35 μ.

On decaying culms of bamboo, Mar. 14, 1897.

The above description is a translation of the original. In view of the figure accompanying the description and the distinctive size and shape of the spores, there should be no doubt as to the identity of this species.

16. Helicoma palmigenum (Penzig & Saccardo) Linder, n. comb.

Helicosporium intermedium var. *palmigenum* Penzig & Saccardo, Icon. Fung. Javan. p. 105. 1904.

Colonies effuse, small or confluent, velvety, black. Conidiophores erect, rather stout, filiform, fuliginous, pallid above.

Conidia acrogenous, dilute fuliginous, the filament coiled two times, 10–12-times septate, the filament 11–12 μ thick and forming a coil 36–40 μ in diameter.

On decaying petioles of palms, Horto. Bogor., Dec. 18, 1896.

This specimen, because of the distinctly greater dimensions and the fewer septa of the spores, should be considered a species distinct from *Helicoma intermedium*, and is so recognized here.

17. Helicoma atroseptatum Linder, n. sp.

Plate 23, figs. 7–9.

Effuse, forming a dark brown, hirsute colony. Repent mycelium fuscous, septate, branched. Conidiophores simple, erect or somewhat irregularly bent, occasionally tending to become fasciculate, deep fuscous, the apical cells subhyaline to hyaline, 150–310 × 6.3–7.2 μ, gradually tapering upwards to the thick (2.5–3.6 μ) rounded terminal cells. Conidia pleurogenous on stout, simple or once-branched hyaline teeth, 2.3–3 × 3.6–7 μ, 1¼–2-times tightly coiled, fuscous except for the basal, and frequently the distal, cells, 10–16-times septate, the septa black, the filament 8–11 μ thick, tapering to the truncate basal cell, the terminal cell abruptly rounded; diameter of the coiled conidia 30–35 μ.

On decaying wood and bark. Chile.

This species grows in company with *Helicoma asperothecum*, from which it is readily distinguished by the simple, erect conidiophores and by the characters of the conidia. It most closely resembles *Helicoma perelegans* in its conidial characters, but again the simple erect habit of the conidiophores of this species separates the two.

Specimen examined:

Chile: Correl, on logs in open clearing, December, *Thaxter*, TYPE (F).

18. Helicoma Mülleri Corda, Icones Fung. **1**: 15. *pl. 4, fig. 219.* 1837.

Helicoryne viride Corda, Icones Fung. **6**: 9. *pl. 3, fig. 38.* 1854.

Helicosporium Mülleri (Cda.) Saccardo, Michelia **2**: 129. 1880.

Helicosporium brunneolum Berkeley & Curtis, Grevillea **3**: 51. 1874.
Helicosporium viride (Cda.) Saccardo, Syll. Fung. **4**: 558. 1886.
Helicomyces Mülleri (Cda.) Pound & Clements, Minn. Bot. Studies **9**: 658. 1896.
Helicomyces brunneolus (B. & C.) Pound & Clements, Minn. Bot. Studies **9**: 658. 1896.

Plate 21, figs. 12–20.

Colonies forming an effuse, hirsute, "Citrine Drab" to "Dark Olive Buff" layer. Sterile hyphae creeping, septate, giving rise to erect or suberect, simple or little-, rarely much-, branched conidiophores. Conidiophores translucent, brown at the base, lighter towards the abruptly rounded, subhyaline apices, 45–150 × 5.4–7.2 μ, septate, the septa mostly 9–14.4 μ apart. Conidia pleurogenous, occasionally acrogenous on simple or once, rarely more frequently, branched, stout (1.5–1.8 × 1.8–5.4 μ), cylindrical teeth, 1½–1¾-times coiled, the filament hyaline to dilute fuscous, (5)–7–9–(11)-times septate, 3.6–5.4 μ thick, bluntly rounded at the distal end, tapering to the truncate basal end; diameter of the coiled conidia (14)–16–19 μ.

On decaying bark or wood of deciduous trees.

The names *Helicoma Mülleri* and *H. Curtisii* have been used more or less interchangeably for the two species. They are, however, separated by quite distinct characters of the conidia and conidiophores. *Helicoma Mülleri* is characterized by the somewhat translucent, closely septate conidiophores with abruptly rounded apices; by the conspicuous, stout sporogenous teeth borne laterally on the conidiophores; and by the truncate basal cell of the conidia. *Helicoma Curtisii* is characterized by the very dark, more distantly septate conidiophores of which the apices are rounded-tapering; the inconspicuous sporogenous teeth; and by the acrogenous conidia with the tapering-rounded, recurved basal ends. The type of *Helicosporium brunneolum* differs in no way from this species, although the conidia were lacking; the conidiophores are typical of those of *Helicoma Mülleri*.

Specimens examined:

Exsiccati: Roumeguere, Fungi Gall. Exsicc., 2133; Bartholomew,

Fungi Columb., 1624; Ellis, Fungi N. J., 3163; Cooke, Fungi Brit. Exsicc. 2nd ed., 447; Jaap, Fl. d. Prov. Brandenb.; Vize, Microfungi Brit., 62.

England: Forden, *J. E. Vize*, in Cooke, Fungi Brit. Exsicc.; North Whitby, Sept. 1900, *S. Crossland* (K).

France: Isere, *J. Thiery, 6508*, in Roumeguere, Fungi Gall. Exsicc; Montmorency, *Boudier, 900* (P).

Germany: Brandenburg, Aug. 1908, *O. Jaap* (B).

United States:

Maine: York, Mt. Agamenticus, on *Quercus*, Sept. 20, 1892, *Thaxter* (F); York, on *Acer rubrum*, Sept. 2, 1891, Sept. 22, 1892, and Sept. 1896, *Thaxter* (F); Kittery Point, on *Pyrus Malus*, Sept. 19, 1892, and on *Quercus*, Aug. 1920, *Thaxter* (F).

Massachusetts: Canton, on chestnut bark, *Linder, 745,1002*; on poplar, Nov. 1924, *Linder* (L); Waverley, on *Acer rubrum*, *Thaxter* (F).

Connecticut: West Haven, Nov. 4, 1888, and Nov. 10, 1888, *R. Thaxter* (F); New Haven, on *Acer*, Sept. 1920, *Thaxter* (F).

New York: Karner, on fallen limbs of *Populus grandidentata*, Oct. 1928, *H. D. House* (MBG 54378).

New Jersey: Newfield, on maple, *J. B. Ellis*, in Fungi N. J.

19. Helicoma proliferens Linder, n. sp.

Plate 22, figs. 6–10; plate 31, fig. 6.

Colonies "Sepia" to "Brownish Olive," round to elongate, 1–4 mm. broad, larger by confluence, finely hirsute. Conidiophores simple or rarely branched, occasionally anastomosing, fuscous except for subhyaline terminal cells, septate, 75–175 × 5–6.5 μ, bearing laterally stout, hyaline to subfuscous, simple or branched teeth 2–5 μ thick. Conidia hyaline, 3–7–(11)-times inconspicuously septate, the filament coiled 1¼–2-times, 5–6.5–(7) μ in diameter, tapering towards the truncate basal end, bluntly rounded at the distal end; the coiled spore 17–24 μ in diameter.

On decaying bark of *Acer*. Connecticut.

This species closely resembles *Helicoma Mülleri* both in the characters of the conidia and conidiophores. The conidia differ from those of the preceding species in that the diameter of the

conidial filament is larger, as is also the diameter of the coiled spore. The proliferating teeth, also, make an additional point of difference. Furthermore, there are present in the type collection, the "sclerote pedicelée" shown in fig. 6 of plate 22.

Specimen examined:

United States:

Connecticut: West Haven, Nov. 10, 1888, *R. Thaxter*, TYPE (F).

20. Helicoma ambiens Morgan, Cinci. Soc. Nat. Hist. Jour. **15:** 46. *fig. 10.* 1892.

Plate 21, fig. 11; plate 23, figs. 1–3.

Helicosporium ambiens (Morg.) Saccardo, Syll. Fung. **11:** 639. 1895.

Colony an effuse, hirsute, "Sepia" layer. Sterile mycelium repent, fuscous, septate, and branching. Conidiophores bent-ascending, occasionally repent, branched, occasionally anastomosing, fuscous except for dilute fuscous terminal cells, 3.5–6 μ in diameter and up to 200 μ long. Conidia acro-pleurogenous, borne singly on short, inconspicuous hyaline teeth, the filament hyaline to dilute fuscous, tightly coiled 1½–1¾ times, 6–8-times septate, 5.4–6.3 μ thick; coiled conidia 18–20 μ in diameter.

On decaying bark. Ohio.

Morgan says of this species that the spores are at first hyaline and continuous and that the septa appear one after another until the spore is 8-septate. In older specimens the spores become brownish-tinged and have added a few half septa so as to appear 9–12-septate.

Although this species very closely resembles *Helicoma Curtisii*, it is characterized by its branching habit. It may also be separated from that species by the additional characters of the conidia; the conidia of *H. Curtisii* having recurved, rounded-tapering basal ends, while those of *H. ambiens* are recurved and bluntly rounded, as will be seen in fig. 11 of plate 21 and fig. 3 of plate 23. The real status of this species can only be determined by comparative cultural studies or else by connecting it with the perfect stage.

Specimens examined:
United States:
Ohio: Preston, *A. P. Morgan*, CO-TYPE (F); TYPE (Ia?).

21. Helicoma asperothecum Linder, n. sp.

Plate 23, figs. 4–6.

Colonies hirsute or stiff-velvety, "Sepia" to almost black, effuse. Conidiophores at first erect, simple, later loosely branched, anastomosing, and tending to become loosely fasciculate, fuscous with dilute fuscous or subhyaline terminal cells, the younger cells granulate-roughened by crystal-like deposits, or the older covered with a deposit of colored crystalloid material, 55–250 × 5.5–7.5 μ. Conidia hyaline to dilute fuscous, acro-pleurogenous on slender, hyaline, cylindrical teeth 1 × 1–2 μ; conidial filament 1½–1¾-times coiled, 8–10-septate, 4.5–6.5 μ thick, tapering slightly towards the bluntly rounded distal end and towards the slightly recurved rounded-tapering basal end; the coiled conidia 15–18 μ in diameter, immature spores as small as 10 μ in diameter.

On decaying bark and wood. Chile.

This species, although resembling *Helicoma Curtisii* and *H. ambiens*, differs from them in many respects. It differs from both by the roughened walls of the conidiophores; from *H. Curtisii* in its branching habit, the shorter spaces between the septa, and the slight constrictions; from *H. ambiens* by the taller and more robust conidiophores, their more erect habit, and the more numerous septa and the tapering, slightly recurved, bluntly pointed basal end of the conidia.

Specimen examined:
Chile: Correl, *R. Thaxter*, TYPE (F).

22. Helicoma conicodentatum Linder, n. sp.

Plate 24, figs. 5–6.

Colonies small, effuse, somewhat arachnoid, "Olive Ocher" to "Olive Yellow." Conidiophores less than 5 μ in diameter, fuscous in the basal portions, hyaline at the extremity, at first simple, erect, then branched, becoming elongate, bent, and tenuous, producing lateral conical swellings on the lower portions, these bearing spores on slender sporogenous teeth. Conidia in

the younger stages acrogenous, later pleurogenous, hyaline to dilute yellowish ochraceous, the conidial filament $1\frac{1}{4}$–$1\frac{3}{4}$-times tightly coiled, 5–7-septate, 5–5.5 μ thick, bluntly rounded at the distal end, rounded-tapering at the frequently apiculate basal end; diameter of the coiled conidia 14–17.5 μ.

On decaying wood. Grenada.

Specimen examined:

Grenada, B. W. I.: Grand Etang, *Thaxter*, TYPE (F).
Trinidad, B. W. I.: Maraval Valley, *Thaxter* (F).

23. Helicoma recurvum (Petch) Linder, n. comb.

Helicosporium recurvum Petch, Roy. Bot. Gard. Peradeniya, Ann. **10**: 138. 1926.

Plate 24, figs. 7–11.

Colonies black, hirsute, effuse, more or less circular. Conidiophores clustered or gregarious, up to 200 μ long, 6–8 μ thick, fuscous except for subhyaline terminal cells, septate, with scattered superficial masses of purplish-black crystalloid deposits, occasionally constricted above and the upper cells often ascending-arcuate. Conidia hyaline or dilute fuscous, acro-pleurogenous, (3)–6–8-septate, not constricted at the hyaline septa, 1–$1\frac{3}{4}$-times coiled, the filament 6–8–(10) μ thick, bluntly rounded at the distal end, rounded-tapering and recurved at the basal end, coiled conidia 15–17–(20) μ in diameter.

On dead mango branches, Ceylon.

H. recurvum closely resembles *H. Curtisii.* The spores of the former, however, are characterized by their thicker filaments which measure 6–8 μ as against 4.5–6.5 μ of *H. Curtisii.* Additional characters for the separation of the two species are to be found in the conidiophores. The lateral sporogenous teeth are more pronounced in this species, and the constrictions and the ascending-arcuate terminal portions of the conidiophores, together with the purplish-black deposits, give additional means for separating the two species.

Specimen examined:

Ceylon: Peradeniya, *T. Petch, 4334,* TYPE (K, Pe, and slide F).

24. Helicoma Curtisii Berkeley, Grevillea **3**: 106. 1875.

Helicosporium Curtisii (Berk.) Saccardo, Syll. Fung. **4**: 560. 1882.

Helicomyces Curtisii (Berk.) Pound & Clements, Minn. Bot. Studies **9**: 659. 1896.

Helicosporium Tiliae Peck, Torr. Bot. Club Bull. **34**: 103. 1907.

Plate 21, figs. 1–10; plate 30, fig. 1; plate 31, fig. 2.

Colonies effuse, hirsute, "Brownish Olive" to "Sepia." Conidiophores erect, simple or rarely branched, up to 200 μ long, 5.4–7.2 μ thick, slightly flexuous, deep fuscous except for the lighter-colored, obtusely rounded-tapering terminal cells. Conidia acrogenous, less frequently pleurogenous, on short slender, inconspicuous teeth, subhyaline to dilute fuscous, 1¼–1¾-times coiled, 4–9-septate, the filaments 4.5–5.4–(7.5) μ thick, the base tapering-rounded and somewhat recurved; diameter of the coiled spore 14.4–18–(20) μ.

On decaying wood and bark of deciduous trees. Early spring to late fall. Europe, and the United States west to Missouri.

Helicoma Mülleri, as is stated in the discussion under that species, has been confused with this. The type specimen of *Helicosporium Tiliae* from Missouri differs from *H. Curtisii* only in the slightly larger spores, the filaments of which are 6.3–7.2 μ thick, and the diameter of the coiled spores varies from 16.2 to 20 μ. Since the spores are alike in all other respects, it seems advisable to classify that species under *Helicoma Curtisii*, especially in view of the fact that in the specimen from Florida, collected by Dr. Thaxter, the spores were even larger, the diameter of filament being 7–8 μ and of the coiled spore 18–22 μ. This specimen, however, was found to be connected with a perfect stage which agrees in all details with *Lasiosphaeria pezizula*, the ascigerous phase in the life history of *Helicoma Curtisii*, as has been demonstrated in Part I of the present paper.

Specimens examined:

Exsiccati: Roumeguere, Fungi Select. Exsicc., 5499, as *Helicosporium vegetum;* Ellis, N. Am. Fungi, 967; Ravenel, Fungi Exsicc., 305.

France: Saint-Bonnet-le-Froid, Dec. 1887, *J. Thierry*, in Roumeguere, Fungi Select. Exsicc.

United States:

Maine: Kittery Point, with *Lasiosphaeria pezizula, Thaxter;* Aug. 1891, *Thaxter* (F); York, on bark of *Populus, Thaxter* (F).

New Hampshire: Bartlett, April, 1901, *Thaxter;* Intervale, on *Acer*, Aug. 1901, *Thaxter* (F).

Massachusetts: Canton, *Linder, 1209*, with *Lasiosphaeria pezizula, 1341, 1047* (L); Sharon, on white oak bark, *A. P. D. Piguet* (F); Lexington, on apple, *Thaxter* (F); Waverley, *Thaxter* (F).

Connecticut: West Haven, on *Acer*, Nov. 1888, *Thaxter;* Tyler City, *Thaxter* (F).

South Carolina: Aiken, *H. W. Ravenel*, in Ellis, N. Am. Fungi.

Florida: Cocoanut Grove, on dead stem of Oleander, with *Lasiosphaeria pezizula, Thaxter* (F); on decaying wood, January, 1898, *Thaxter* (F).

Missouri: Emma, September, 1906, *Demetris*, type of *Helicosporium Tiliae* (NYS, slide MBG, F).

The perfect stage of this fungus is *Lasiosphaeria pezizula.* The description follows:

Lasiosphaeria pezizula (B. & C.) Saccardo, Syll. Fung. **2**: 195. 1883.

Sphaeria pezizula Berkeley & Curtis, Grevillea **4**: 106. 1876.

Herpotrichia pezizula (B. & C.) Ellis & Everhart, N. Am. Pyrenomycetes, p. 160. 1892.

Perithecia gregarious, black, smooth at maturity, pear-shaped when moist, concave or cup-shaped when dry, 350–400 μ in diameter. Asci clavate to broad-clavate, 18–27 × 107–155 μ, the distal end thickened, each end penetrated by a single pore through which the ascospores escape. Spores secreted in a mass at the mouth of the ostiole, at first hyaline and then dilute fuscous, 5–7-septate, 30–55 × 5–7 μ, straight or slightly curved, tapering from the middle towards the rounded or somewhat pointed ends.

Habitat as in the imperfect stage.

Ellis and Everhart report the ascospores as being occasionally 8–10 μ thick, and further state that "Cooke in his Synopsis places this among the brown-spored species, but we have always found the sporidia hyaline." This statement is an additional example of the confusion that is likely to arise when color is used as a basis for the separation of genera. The spores of this species when first extruded are, as Ellis and Everhart point out, hyaline,

but when they have been exposed to the air only a few days, they become light fuscous, even though viewed under the microscope.

Specimens examined in which the perfect and imperfect stages occur together:

United States:

Maine: Kittery Point, *R. Thaxter* (F).

Massachusetts: Canton, *Linder, 1209* (F, L, MBG).

Florida: Cocoanut Grove, *R. Thaxter* (F).

25. **Helicoma fasciculatum** Berkeley & Curtis, in U. S. North Pacific Exped., No. 142.

Helicosporium fasciculatum (B. & C.) Saccardo, Syll. Fung. **4**: 560. 1886.

Helicomyces fasciculatus (B. & C.) Pound & Clements, Minn. Bot. Studies **9**: 658. 1896.

Plate 24, figs. 3–4.

Colonies as small, brownish-black, circular patches on the under side of leaves. Conidiophores arising in clusters from gatherings of dark hyphae in the substratum, erect or slightly flexuous, simple, fuscous, the apical cells subhyaline, 63–243 × 2.8–3.6 μ, the conidia acrogenous, produced singly or in pairs, at first hyaline then dilute fuscous, 3–5-septate, a dark line being formed on either side of the septa, spore filament 7.2 μ thick, once-coiled to form conidia 12.5–14.5 μ in diameter.

On the under side of dead leaves, Loo-Choo Islands, Japan. This species is also reported from California by Harkness[1] on leaves of *Laurus* sp.

Specimen examined:

Exsiccati: U. S. North Pacific Expedition, under Commanders Ringgold and Rogers, 1853–56. Loo-Choo Islands, Japan, *C. H. Wright, 142*, TYPE.

26. **Helicoma simplex** (Sydow) Linder, n. comb.

Helicosporium simplex Sydow, Herb. Boissier Mem. **4**: 7. 1900.

Plate 24, figs. 1–2.

[1] Harkness, H. W., in Cooke & Harkness, Grevillea **9**: 85. 1881.

Colonies as brownish-black circular patches on the under side of leaves. Conidiophores arising in clusters from gatherings of dark hyphae in the substratum, erect or ascending, simple or rarely branched, fuscous, the terminal cells hyaline, 27–100 × 3.3–4.5 μ, the tip inflated and bearing conidia singly. The conidia at first hyaline, then dilute fuscous, apical or occasionally lateral on swellings of the conidiophores, 3–4-septate, the septa bordered on either side by dark lines, once-coiled, flat, the filament 5–6 μ thick; the conidia 9–12 μ in diameter.

On under side of leaves of *Daphniphyllum macropodium*. Japan.

This species differs from *Helicoma fasciculatum* in its shorter, more robust, and lighter-colored conidiophores; by the presence of lateral swellings on these, resulting from their continued growth after the first spores have been produced; and also by the fact that the spores, smaller in size, are borne singly. This species and the preceding are quite characteristic and form a group which appears to be oriental. The spores of *Helicostilbe simplex* resemble those of the two above species; the conidiophores, however, are aggregated to form the stelar structure characteristic of the Stilbaceae.

Specimen examined:
Japan: Nishigahara, *Kusano*, TYPE (S, slide F).

SPECIES IMPERFECTLY KNOWN

Helicoma candidum (Pr.) Linder, n. comb.

Helicotrichum candidum Preuss, Linnaea **24**: 111. 1851.

Helicomyces candidus (Pr.) Saccardo, Syll. Fung. **4**: 234. 1886.

Plate 24, fig. 12.

"Thallo effuso albo; sporis flocciformibus, apice et lateribus surculatis, spiraliter convolutis septatis diaphanis albis.

"Habitat in asseribus antiquis, foliisque dejectis Pini. Hoyerswerda."

In the original description given above there is little to identify this species. Fresenius[1] gives a more ample definition of the species as follows:

[1] Fresenius, G. Beitrage z. Myk. 3: 101. *pl. 12, fig. 31–33*. 1863.

"Preuss theilt in der Linnaea von 1851 dieser seiner neuen Art, welche ich aus Rabenhorst's herbar. mycol. Nr. 1434 kenne, einen thallus effusus albus zu. An den mir vorliegenden Exemplaren konnte ich einen Träger der Sporen nicht auffinden; er ist vielleicht nur sehr kurz, wohl auch zart und vergänglich. Die Sporen sind 1/60–1/40 mm. gross, weiss, mit einem kurz vorgezogenen abgestutzten Spitzchen. Scheidewände öfter schwer wahrzunehmen, nicht so zahlreich wie bei dem vorigen Pilz [*Helicoma phaeosporium*]; ich zählte deren 3–5, seltner auch wohl fast die doppelte Anzahl. Figur 31–33 [above] sind drei Sporenexemplare nach einer 350 maligen Vergrösserung abgebildet."

Fig. 13. *H. candidum.* After Fresenius.

In number 1434 of Rabenhorst's 'Herbarium Mycologicum' at the Farlow Herbarium, the writer was able, after diligent searching, to find but one spore, and this corresponded very well with that figured by Fresenius. That the species is neither a *Helicomyces* nor *Helicotrichum* is clearly shown by the relative stoutness of conidial filament which definitely places the species in this genus. Unfortunately, owing to the lack of details concerning the conidiophores, it is impossible to give the species a definite place among the other better-known ones, although, because of its habitat and the nature of its spores, it appears to be quite distinct. The following are the characters noted for the one spore: spore hyaline, once-coiled, 3-septate, the filament 9 μ thick, rounded-tapering to a somewhat truncate basal end, the distal end bluntly and obtusely rounded; diameter of the coiled conidium 18 μ.

XENOSPORELLA

Xenosporella von Höhnel [ed. Weese], Centralbl. f. Bakt. Abt. II. **60:** 17. 1923.

Helicoma Sacc. nec. Corda, Saccardo, Syll. Fung. **11:** 638. 1895.

Colonies stiff-velvety, brown or black. Conidiophores short, stout, hyaline to deep fuscous, branched. Conidia 1–1½-times coiled, dilute fuscous to deep fuscous, the filament thick, non-hygroscopic, longitudinally and transversely septate.

The type species is *Xenosporella pleurococca.*

The fundamental character of this genus is the longitudinally and transversely septate spores. Until von Höhnel established this genus, the species were classified under *Helicoma, Helicosporium,* and *Helicomyces.*

KEY TO THE SPECIES OF XENOSPORELLA

1. Conidia 38–55 μ in diameter, deep fuscous to opaque and black. . *3. X. Thaxteri*
1. Conidia less than 35 μ in diameter. 2
2. Mature conidia fuscous to deep fuscous, the filament coiled around a central cell. 3
2. Mature conidia subhyaline to dilute fuscous, the filament not, or rarely, coiled around a central cell. . . . . *4 X. larvalis*
3. Conidiophores hyaline to subhyaline, or if fuscous, only at the base. . . . . *1. X. pleurococca*
3. Conidiophores deep fuscous. . . . . *2. X. Berkeleyi*

1. **Xenosporella pleurococca** von Höhnel [ed. Weese], Centralbl. f. Bakt. Abt. II. **60:** 17. 1923.

Plate 25, figs. 1–5.

Colonies effuse, short-velvety, dusty-gray to black. Sterile mycelium repent, fuscous or brown, septate, branched. Conidiophores hyaline or subhyaline, stout, erect, branching below, 18–45 × 3.5–4.5 μ. The conidia acrogenous, at first subhyaline, at maturity becoming fuscous, $\frac{3}{4}$–1-coiled, longitudinally and transversely septate, dividing the conidium into 13–16 cells, the filaments 12.5–17 μ thick, coiled around darker-colored central cells, the coiled conidia 24–30 μ in diameter.

On decaying wood of *Populus.* Austria.

Specimen examined:

Austria: Sonntagsburg, *von Höhnel, 2664,* TYPE (F).

2. **Xenosporella Berkeleyi** (Curtis) Linder, n. comb.

Helicoma Berkeleyi Curtis, Am. Jour. Sci. II. **6:** 352. 1848.

Helicoma binale Curtis, in Berkeley & Curtis, N. Am. Fungi, 3297.

Helicoma binale var. *apertum* Curtis, *Ibid.*

Helicosporium Berkeleyi (Curtis) Saccardo, Syll. Fung. **4:** 560. 1886.

Helicosporium binale (Curtis) Saccardo, *Ibid.*
Helicosporium diplosporum Ellis & Everhart, Acad. Phila. Proc. **1891**: 93. 1891.
Helicomyces diplosporus (E. & E.) Pound & Clements, Minn. Bot. Studies **9**: 659. 1896.
Helicoma bambusae P. Hennings, Hedwigia **41**: 310. 1902.

Plate 25, figs. 6–11.

Colony effuse, coarsely granular to short, coarse-velvety, olive-black to black. Conidiophores much-branched, septate, dark brown, short and stout, 36–144 × 3.6–7.2 μ. Spores acrogenous, dilute fuscous to very deep fuscous, ¾–1-coiled, longitudinally and transversely septate, dividing the spores into 13–22 cells, the filaments 9.5–11.5 μ thick, coiled around darker central cells, the coiled conidia 23–27 μ in diameter.

On bark and wood of deciduous trees and vines, and on bamboo. Southern United States, the West Indies, and Brazil. Also reported from India.

This tropical or subtropical species, because of its exceptional appearance, has received a number of names. An examination of the types of *Helicosporium diplosporum* and of *Helicoma bambusae* indicates that all these species are identical with the type of *Helicoma Berkeleyi* and are synonymous. *Helicoma binale* and its variety *apertum* were distributed by Curtis in the 'North American Fungi,' but were not actually published until they appeared in the 'Sylloge Fungorum.' Curtis, however, did publish *H. Berkeleyi*, and in a subsequent number of the 'American Journal of Science'[1] stated that the species and variety were the same as *H. Berkeleyi* which he published earlier. He also tentatively proposed the new genus *Systrephium* but failed to describe it.

Specimens examined:

Exsiccati: Ravenel, Fungi Caroliniani, IV, 85.

United States:

South Carolina: Society Hill, on *Cornus florida*, *Curtis*, TYPE (F, BM, P); on *Platanus*, *Ravenel*, *3297*, as *Helicoma binale* (BM); Pinesville, on *Liquidambar*, *Ravenel*, *X4;* no locality, on *Rhus radicans*, *Ravenel*, *1203* (BM).

[1] Curtis, M. A. Am. Jour. Sci. II. **6**: 444. 1848.

Georgia: Darien, on *Arundinaria*, *Ravenel*, *2508* (BM); on *Liquidambar*, *Ravenel*, *3210* (BM).

Florida: Gainesville, on *Carpinus*, *Ravenel*, *89* (BM); on *Aralia spinosa*, *Ravenel*, *112* (BM); Cocoanut Grove, on dead stems of Oleander, *Thaxter* (F); Grasmin, on old palmetto, *Sturgis*, as *Helicoma larvale* (F).

Alabama: Montgomery, *Burke*, *368* (MBG).

Tennessee: Burbank, on *Cornus*, *Thaxter* (F).

Louisiana: St. Martinsville, on *Vitis vulpina*, *Langlois*, type of *Helicosporium diplosporum*, also under the name of *Helicoma velutinum* (F).

Bermuda: on palmetto, Acad. Nat. Sci. Phila. Expl. Bermuda, 1380-C, as *Helicoma larvale* (NY).

Trinidad: Port-of-Spain, Maraval Valley, on bamboo, *Thaxter* (F).

Brazil: Sao Paulo, on bamboo, *Putteman*, *350*, type of *Helicoma bambusae* (B, S).

A perfect stage, *Melanomma helicophilum* (Cke.) Sacc., was suggested by Cooke[1] as being connected with *Helicoma Berkeleyi*, but such a connection is extremely doubtful, as is also the identity of the ascigerous stage. Berlese[2] states in regard to *Melanomma helicophilum*, "Ex specim. orig. nihil eruere potui. Certe ut videtur species non ad *Melanomma* pertinet." The writer was unable to find *Sphaeria helicophila* Cke. (*Melanomma helicophila*) in Ravenel's 'Fungi Americani,' although in his 'Fungi Caroliniani' a perfect stage was found with the material labelled *Helicoma Berkeleyi*. This proved to be *Lasiosphaeria pezizula*, and with it, although *H. Berkeleyi* was also present, were the conidiophores of *Helicoma Curtisii* forming a part of the thin subiculum. Conidia of the latter were also present. It therefore would appear from above evidence that *Sphaeria helicophila* Cke., *Byssosphaeria helicophila* Cke., and *Melanomma helicophilum* (Cke.) Sacc. are identical with *Lasiosphaeria pezizula* (B. & C.) Sacc. and should be considered synonymous with that species.

3. **Xenosporella Thaxteri** Linder, n. sp.

Plate 25, figs. 16–24.

Colonies effuse, black, coarsely pulverulent. Conidiophores

[1] Cooke, M. C. Grevillea **6**: 145. 1878.

[2] Berlese, A. N. Icones Fung. **1**: 38. 1890.

hyaline to subfuscous, arising from branched, repent, subfuscous mycelium, 15–25 × 4–5.4 μ. Conidia acrogenous or apparently pleurogenous on short, tooth-like branches, transversely septate, and somewhat spirally coiled, at maturity becoming 28–65-celled from the longitudinal and transverse septa, deep brown to opaque brownish-black, hyaline when immature, tapering from 20–25 μ at the center to 10–13 μ at the thick truncate basal end, and to the rounded acuminate, often hyaline, distal cell, the coiled conidia 37–57 μ in diameter. Secondary conidia hyaline, pear-shaped, 2-celled, the basal cell smaller, 11 × 19.5 μ, borne acrogenously on fuscous, simple, septate conidiophores, 80–100 × 3.6–4.5 μ.

On dead *Costus spiralis* stems. Trinidad, B. W. I.

This species is dedicated with great pleasure to Dr. Roland Thaxter of Harvard University, not only because he collected it, but also as a token of gratitude for the privilege of studying his extensive collection of helicosporous forms.

It is scarcely necessary to say anything further of this remarkable and striking species. Its characters are sufficiently definite to preclude the possibility of its being confused with any species heretofore described. It should be mentioned, however, that there is evidence of further polymorphism, but since this could not be proven definitely, it seems advisable to pass over the doubtful stages with the hope that this species will again be collected and will then be grown in culture. In association, although not definitely connected with the above species, is a perithecial stage which is described as follows:

Acanthostigmella Thaxteri Linder, n. sp.

Perithecia solitary or widely scattered, rounded pear-shaped, 90 × 79 μ, peridium leathery, dilute fuscous, the ostiole encircled by an irregular row of short, stout, erect, bent or recurved bristles, 27–36 × 3.6 μ. Asci 36–45 × 7.2 μ, 8-spored. Spores 4–5-septate, at first hyaline, then subfuscous, straight or slightly curved, 15–20 × 3–3.5 μ, broadest at the middle, rounded at the ends.

Specimen examined:

Trinidad, B. W. I.: Maraval Valley, Port-of-Spain, on dead *Costus spiralis*, *Thaxter*, TYPE (F).

4. **Xenosporella larvalis** (Morgan) Linder, n. comb.
Helicoma larvale Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 45. *fig. 9.* 1892.

Plate 25, figs. 12–15.

Colony effuse, thin, pulverulent, dirty gray or brownish. Conidiophores branched, septate, hyaline or dilute fuscous above, light fuscous to fuscous at the basal cells, short, stout, up to 75 μ long, 3.2–4.5 μ thick, arising from fuscous repent, septate, and branched sterile hyphae. Conidia acrogenous, hyaline to dilute fuscous in the old spores, once-coiled, longitudinally and transversely divided into 15–18–(20) cells by colored septa, the filament 6.5–8 μ thick, abruptly rounded at the distal end, and tapering to a broad truncate basal end, rarely coiled around a central hyaline cell; diameter of coiled spore 15.5–20 μ.

On decaying woody substances. Ohio and North Carolina.

This species, because of the hyaline to subhyaline conidia which are divided by dark septa and because of the dimensions of the conidia and conidiophores, is quite distinct from other members of the genus. Doubt as to the identity of the species has resulted from the fact that Morgan distributed or determined a few specimens under this name which in reality are obviously *X. Berkeleyi.* Material kindly communicated to me by Dr. G. W. Martin from the Morgan herbarium in the University of Iowa, however, definitely decides the status of this species.

Berlese[1] has figured *Chaetosphaeria parvicapsa* (Cke.) Sacc. as the perfect stage of this species. The measurements of the conidia are slightly larger than those given here. He states that the conidia of his material, collected in Aiken, North Carolina, measure 18–22 μ in diameter.

Specimen examined:
United States:
Ohio: on inner bark of *Acer saccharinum, A. P. Morgan,* TYPE (Ia, and slides F, MBG).

HELICOON

Helicoon Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 50. 1892; Saccardo, Syll. Fung. **11**: 609. 1895; Lindau, in Engl. & Prantl,

[1] Berlese, A. N. Icones Fung. **1**: 27. *pl. 17, fig. 4.* 1890.

Nat. Pflanzenfam. **1** (1**): 452. 1900; Lindau, in Rabenhorst, Kryptog. Fl. Deutschl. Öst. u. d. Schweiz **1**[8]: 535. 1906; **1**[9]: 277. 1908.

Type species is *Helicoon sessile* Morgan.

Conidiophores various, erect, simple or branched, or apparently obsolete. Conidia hyaline, bright-colored, or fuscous, the filament coiled in 3 planes to form a cylindrical or ellipsoidal body, never in chains.

Before the creation of this genus, members of the group were classified under *Helicoryne*, *Helicomyces*, and *Helicosporium*. As at present constituted, *Helicoon* is a homogeneous group characterized by the cylindrical or ellipsoidal spore bodies and shows no transitional tendencies towards any other genera with the exception of *Helicodendron*, from which genus it is separated by the conidia not being in chains, but produced singly. It should be emphasized that a very careful examination should be made to determine this point, since in certain species of *Helicodendron*, the spores fall apart very readily.

KEY TO THE SPECIES OF HELICOON

1. Conidiophores less than 50 μ long....................2
1. Conidiophores more than 50 μ long....................4
2. Conidia fuscous, 50–60 × 50–80 μ....................*1. H. Richonis*
2. Conidia hyaline, smaller....................3
3. Conidia 25–27 × 23–36 μ; filament 3.3–4.5 μ thick, coiled 5–8 times; conidiophore 15–20 × 2–4 μ....................*2 H. farinosum*
3. Conidia 20–30 × 37–56 μ; filament 4.5–6.5 μ, coiled 5–16 times..*3. H. sessile*
4. Conidiophores simple or little-branched....................5
4. Conidiophores much-branched, anastomosing....................6
5. Conidia golden-yellow, 19.5–27 × 36–45 μ....................*4. H. auratum*
5. Conidia hyaline to dilute fuscous, 20–25 × 22.5–33 μ........*5. H. fuscosporum*
6. Conidia 18–27 × 28–45 μ, the filament 4.5–5.4 μ............*6. H. ellipticum*
6 Conidia 16.2–18 × 18–24 μ, the filament 2.3–3.6 μ.......*7. H. reticulatum*

1. Helicoon Richonis (Boudier) Linder, n. comb.

Helicosporium Richonis Boudier, Icon. Myc. **4**: 349. *pl. 599.* 1905–10.

Small species, blackening by its extent the wood on which it grows. Sterile hyphae repent, septate, blackish, giving rise to short concolorous filaments, also septate, bearing a large conidium irregularly oval or rounded, formed of a brown filament,

multiseptate, 50–60 × 50–80 μ, 8–10-seriate. The height of the conidiophore does not exceed 1–1.5 μ.

On dead branches of *Populus*. Department of the Marne, *Richon*.

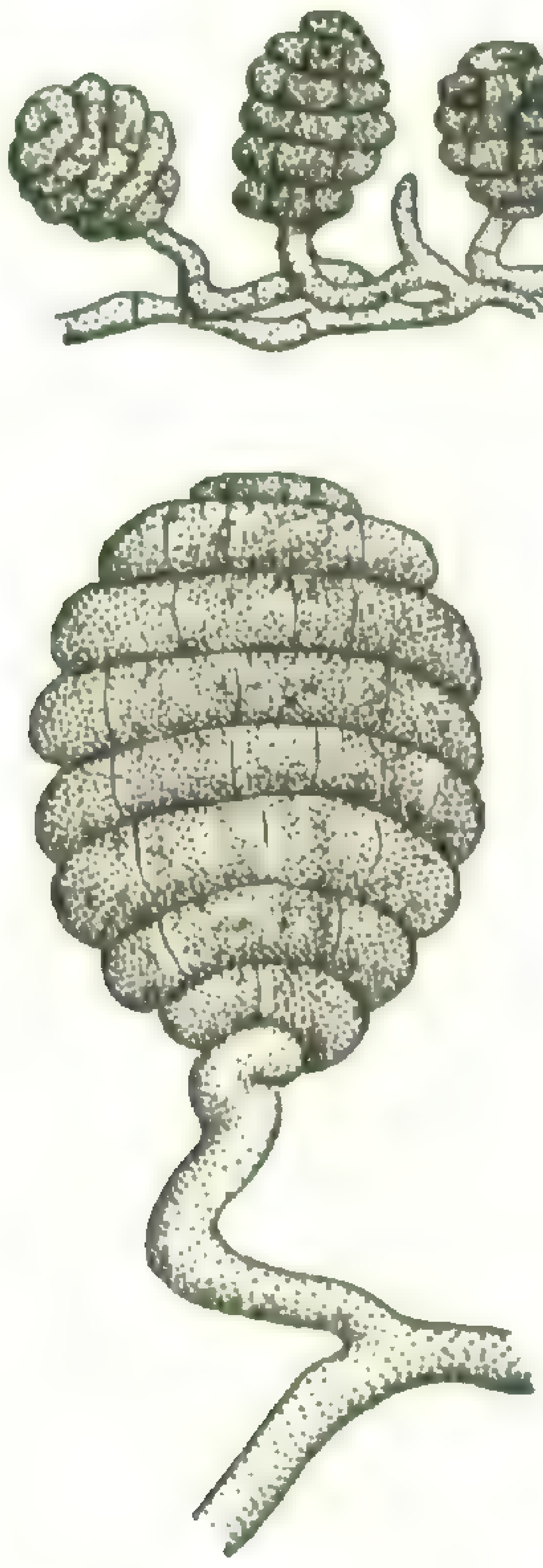


Fig. 14. *H. Richonis*. After Boudier.

The above description is adapted from the original and the figure is after the colored original illustration.

The species is quite distinctive in its color and size, and in the morphology of the conidiophore.

2. **Helicoon farinosum** Linder, n. sp.

Plate 26, figs. 1–2.

Colonies inconspicuous, white, powdery. Conidiophores hyaline, inconspicuous, 15–20 × 2–4 μ, tapering upwards. Conidia acrogenous, hyaline, the filament 3.5–4.5 μ thick, coiled 5–8 times in 3 planes to form a subglobose to ellipsoidal spore body, 23.4–36 × 25–27 μ.

On decaying wood. Massachusetts.

This species very strongly resembles *Helicoon sessile*, yet differs

in the smaller size of the spore, and by the fact that the cytoplasmic content is less dense and the septa more conspicuous.

Specimen examined:

United States:

Massachusetts: Cambridge, Fresh Pond, Oct. 11, 1892, *Thaxter*, TYPE (F).

3. **Helicoon sessile** Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 50. *fig. 17.* 1892.

Helicoon Fairmani Saccardo, Ann. Myc. **4**: 278. 1906.

Plate 26, figs. 12–16.

Colonies pulverulent, inconspicuous, white to pinkish, sparsely covering the substratum. The conidiophores in culture seldom exceeding 50 μ in length, apparently obsolete on the natural substratum. Conidia acrogenous, borne singly, hyaline to pinkish, the filament (4)–4.5–6.5 μ thick, coiled 5–16 times in 3 planes to form an ellipsoidal body, 20–30 × 37–59 μ.

On very moist well-decayed wood of deciduous trees. Eastern United States.

The type of this species appears to be material collected by Ellis, presumably in New Jersey, and sent to Morgan under the herbarium name of *Helicosporium conchoides*, a fragment of which specimen was communicated by Morgan to Dr. Thaxter. *Helicoon Fairmani*, collected in New York by C. E. Fairman and sent to Saccardo who described the species as new, differs in no respect from Morgan's.

Specimens examined:

United States:

Massachusetts: Canton, on decaying maple wood, *Linder, 241*, and July 16, 1925, *Linder* (L, F); Sharon, Nov. 1922, *Piguet* (L 252); Waverley, Oct. 2, 1892, and Oct. 4, 1892, *Thaxter* (F).

New Jersey: *Ellis*, comm. to R. Thaxter by Morgan, CO-TYPE (F).

4. **Helicoon auratum** (Ellis) Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 50. *fig. 18.* 1892.

Helicosporium auratum Ellis, Torr. Bot. Club Bull. **6**: 106. 1876.

Plate 26, figs. 3–5.

Colony golden-yellow, effuse, pulverulent. Conidiophores erect, simple or rarely sparingly branched, fuscous below, subhyaline at terminal cells, 32–150 × 3.6–5.4 μ. Spores hygroscopic, borne singly or in clusters, never in chains, acro-pleurogenously on upper subhyaline part of the conidiophores, hyaline to light yellow, the filament 2.5–3.6 μ, coiling in 3 planes to form an ovoid to elongate-elliptical spore body, 8–16-seriate, 36–45 × 19.5–27 μ.

Growing on partly buried and well-decayed wood in moist places. April to November. Eastern United States.

Helicoon auratum is a thoroughly characteristic species differing from all other members of the genus by the brilliant yellow color of the spores, and the characteristic dark erect conidiophores.

Specimens examined:

Exsiccati: Ellis, N. Am. Fungi, 551, TYPE; Reliquiae Farlow., 175, as *Helicosporium aureum.*

United States:

Massachusetts: Billerica, *Piper* (F); Brookline, Hammond's Pond, *Faull* (F); Canton, *Linder, 179, 221, 1018* (F, L, MBG); Sharon, *Piguet* (L 237).

5. **Helicoon fuscosporum** Linder, n. sp.

Plate 26, figs. 6–8.

Colony inconspicuous, sparse, of scattered conidiophores visible only under a hand lens. Conidiophores erect, simple or very sparingly branched above, septate, fuscous below, subhyaline to dilute fuscous above, 70–200 × 4.5–5 μ, slightly tapering upwards to 3 μ, somewhat constricted at the septa. Conidia acrogenous, borne singly, occasionally in pairs, light fuscous, the filament 2.7–3 μ thick, coiling in 3 planes to form 6–9-seriate, subovate to ellipsoidal spore bodies, 20–25 × 22.5–33 μ.

Growing on catkins of *Alnus* sp. Connecticut.

Specimen examined:

United States:

Connecticut: New Haven, May, 1901, *R. Thaxter*, TYPE (F).

6. **Helicoon ellipticum** (Peck) Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 50. *fig. 19.* 1892.

Helicosporium ellipticum Peck, N. Y. State Mus. Rept. **27**: 103. *pl. 2, fig. 9–12.* 1877.

Helicoryne ramosa Berkeley & Smith, in Berkeley, Gard. Chron. N. S. **17**: 463. *fig. 73.* 1882.

Helicosporium ramosum (B. & S.) Massee, Brit. Fung. Fl. **3**: 440. *pl. p. 442, fig. 29.* 1893.

Plate 26, fig. 11; plate 31, fig. 5.

Colony loose, cottony, separable from the substratum, "Brownish Olive." Conidiophores elongate, much branched and anastomosing, up to 800 μ long, 4.5–5.5 μ thick. Spores borne singly on lateral hyaline teeth on the lower two-thirds of the conidiophores or nearer the tips in more mature specimens, "Honey Color" to "Olive Ochre" in mass, the filament 4.5–5.4 μ thick, coiled in 3 planes to form 7–10-seriate, elongate-ellipsoidal or ellipsoidal spore bodies, 18–27 × 28–45 μ.

On decaying coniferous wood in moist shaded places. Spring to fall. Eastern United States.

Specimens examined:

Exsiccati: Ellis, N. Am. Fungi, 124; C. E. Fairman, Mycotheca Fairmani, 1191.

United States:

Maine: Kittery Point, Sept. 26, 1892, with *Helicosporium aureum*, June 30, 1892, Aug. 1892, *R. Thaxter* (F); York, July 9, 1892, *R. Thaxter* (F).

New Hampshire: Intervale, July, 1901, *R. Thaxter* (F).

Massachusetts: Pepperell, Oct. 1926, *C. W. Dodge* (F, MBG, 66537); Waverley, Oct. 1892, *R. Thaxter* (F).

Connecticut: Milford, *R. Thaxter* (F).

New York: in Berkeley Herb., type of *Helicosporium ramosum* (K); Lyndonville, Sept. 1900, *C. E. Fairman*, in Mycotheca Fairmani.

New Jersey: Vineland, *J. B. Ellis*, in N. Am. Fungi, TYPE.

7. Helicoon reticulatum Linder, n. sp.

Plate 26, figs. 9–10.

Colony loose, cottony, separable from the substratum, "Raw Umber" to "Brownish Olive." Conidiophores dilute fuscous to

fuscous, erect, frequently branched and anastomosing to form a complicated network of hyphae up to 800 μ long, 3.6–5.4 μ thick. Spores produced singly and pleurogenously on the lower two-thirds of the conidiophore, on hyaline teeth, the spore filament dilute ochraceous, the first coil often hyaline, 2.6–3.6 μ thick, coiled in 3 planes to form 6–8-seriate, ovoid to ovoid-elliptical spore bodies, 16–18 × 18–24 μ.

On moist decaying wood, generally coniferous. Summer. Maine south and west to Mississippi.

This species closely resembles *Helicoon ellipticum* in the appearance of the colonies and of the conidiophores. The smaller spores, however, separate it from that species. The range is apparently more southern.

Specimens examined:

United States:

Maine: Kittery Point, Sept. 26, 1892, *Thaxter* (F).

Massachusetts: Canton, *Linder, 1010* (L, F).

Connecticut: New Haven, July, 1889, *R. Thaxter* (F).

Alabama: Montgomery, *R. P. Burke, 373* (MBG 57241).

Mississippi: Starkville, Apr. 3, 1889, *G. W. Merrill,* TYPE (F).

SPECIES IMPERFECTLY KNOWN

Helicoon politulum (Schulzer) Lindau in Rabenhorst's Kryptog. Fl. Deutschl., Öst. u. d. Schweiz 1[9]: 277. 1908.

Helicosporium politulum Schulzer, Flora **60**: 271. 1877.

"Räschen schwarzgrau, höchst unscheinbar, mehrere mm. breit. Mycel kriechend, septiert, verzweigt, kaum durchscheinend. Konidienträger gesellig, unverzweigt, aufrecht oder gekrümmt, weitläufig septiert, bisweilen an den Wänden etwas eingeschnürt, bis oben hin gleich dick, schwarzbraun, durchscheinend. Konidien am Ende der Träger zu einer köpfchenartigen Masse zusammengewunden, die in Wasser sich trennt, korkzieherartig oder sprungfederartig gewunden von rechts nach links, dicht septiert, schwarzgrau, durchscheinend.

"Auf feuchten modernden Weidenastspänen bei Vinkovce in Slavonien (Schulzer)."

The above description is Lindau's condensation and interpretation of Schulzer's original description. This species apparently

is not unlike *Helicoon Richonis*. Its identity, however, must remain obscure until spore measurements are available.

HELICODENDRON

Helicodendron Peyronel, Nuovo Giorn. Bot. Ital. N. S. **25**: 460. *figs. 71–76.* 1918.

Helicodesmus Linder, Am. Jour. Bot. **12**: 259–269. *pl. 23–24.* 1925.

Type species of the genus is *Helicodendron paradoxum.*

Conidiophores much-branched to simple or apparently obsolete, hyaline or fuscous. Conidia in chains, coiled in 3 planes to form a cylindrical, ovoid, or ellipsoid spore body, occasionally only few-seriate, then forming an almost disc-shaped body, hyaline, colored, or fuscous.

The most important distinguishing character of this genus is the method of producing spores in chains. The ovoid or elliptical shape of the coiled spore is, in general, fairly constant, although the spores of *Helicodendron paradoxum* and *H. triglitziensis* more closely resemble in shape the spores of species of *Helicoma.*

KEY TO THE SPECIES OF HELICODENDRON

1. Conidia less than 4-seriate; the conidial filament 4 μ or more in diameter....2
1. Conidia more than 4-seriate, if less, then the conidial filament less than 3 μ in diameter..3
2. Conidia 1–5-septate, at first hyaline, then becoming light green. *1. H. paradoxum*
2. Conidia 6–8-, rarely 3–10-, septate, always hyaline.........*2. H. triglitziensis*
3. Conidia 18–22 × 20–32 μ, the filaments 2.5–3.6 μ in diameter. *3. H. tubulosum*
3. Conidia smaller..4
4. Conidia 10.8–14.4 × 14.4–27 μ; the filament 1.5–2.5 μ thick, subhyaline to subfuscous...*4. H. fuscum*
4. Conidia 8–10 × 11 μ; the filament 1.2–1.8 μ thick, hyaline........*5. H. hyalinum*

1. **Helicodendron paradoxum** Peyronel, Nuovo Giorn. Bot. Ital. N. S. **25**: 460. *fig. 71–76.* 1918.

Clusters broadly effuse, pulverulent, at first white, then light and intense green, finally sordid. Sterile mycelium repent, sparsely branched, septate, hyaline, 4–6 μ thick. Conidiophores erect, branching, septate, slightly constricted at the septa, 70–100 × 5–7μ. Conidia coiled 1–3½, mostly 1½–2, times, 1–3-septate, slightly constricted at the septa, the distal end obtuse, at first hyaline to light green, becoming darker with age, prolif-

erating to produce branched chains, the conidial filament 5.5–6.5 μ thick; the coiled conidia 35–40–60 μ in diameter.

On decorticated trunks and branches at the edge of mountain streams, frequent; on *Alnus viridus* (Li Cumbal di l'Truncea, 1400 m. alt.), Aug. 1914; on *Cytisis laburnis* (Li Cumbal da Sere, 1070 m. alt.), Apr. 1916, Riclaretto in the Piedmont Valley, North Italy.

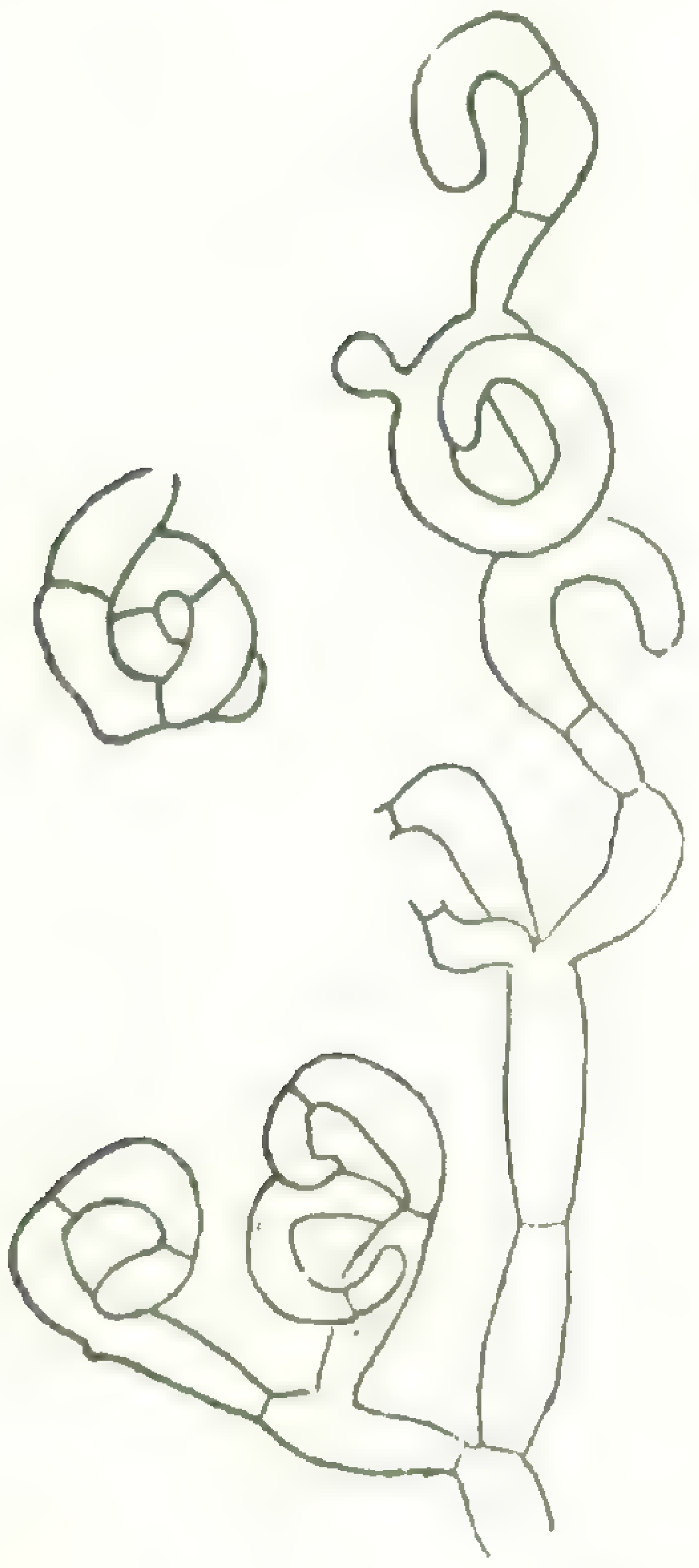


Fig. 15. *H. paradoxum.* After Peyronel.

2. **Helicodendron triglitziensis** (Jaap) Linder, n. comb.

Helicomyces triglitziensis Jaap, Verhandl. Bot. Ver. Prov. Brandenb. **58**: 43. 1916.

Helicodesmus albus Linder, Am. Jour. Bot. **12**: 259–269. *pl. 23–24.* 1925.

Plate 27, figs. 1–2; plate 30, fig. 4.

Colonies as white flocculent tufts on the substratum. Vegetative hyphae hyaline, septate, and much-branched. Conidiophores arising singly as short hyaline, mostly simple aerial branches bearing conidia acro-pleurogenously. Conidia in branching chains, hyaline, 1¾–2¾-times convolute, 6–8-, seldom 3–10-, septate, smooth, slightly constricted at the septa; the filament rounded-tapering at the basal end, the distal end bluntly rounded, 3.6–6.2 μ thick; the coiled conidia 16.2–25.4 μ in diameter.

Specimens examined:

Exsiccati: Jaap, O., Fungi Select. Exsicc., 847.

Germany: Triglitz, *Jaap*, in Fungi Select. Exsicc., TYPE.

United States:

Massachusetts: Fresh Pond, Cambridge, *W. H. Weston*, type of *Helicodesmus albus* (F); Fresh Pond, *Linder, 291* (L).

3. **Helicodendron tubulosum** (Reiss) Linder, n. comb.

Helicomyces tubulosus Reiss, Beitr. Pilzk. **11**: 140. *pl. 3, fig. 11–13.* 1853.

Helicoon tubulosum (Reiss) Saccardo, Syll. Fung. **11**: 609. 1895.

Plate 27, figs. 7–11.

Colonies as shining white, scattered, minute granular tufts of spores on the surface of the substratum. Conidiophores inconspicuous, 0–50–100 × 3.5–5 μ. Conidia acrogenous, in branching chains, 4–12-times coiled to form cylindrical to ellipsoidal bodies, 18–22 × 20–32 μ, the filaments 2.5–3.6 μ thick.

On decaying *Salix* twigs and bark in moist places. Europe and America.

As illustrated by Cooke,[1] the conidium is coiled to form a rounded cone-shaped body, the filaments of which are deeply constricted at the septa, thus giving it a toruloid appearance. When the writer examined the specimen, deposited in the Kew Herbarium, there were no spores. It seems probable, however, that the figure as shown was drawn from spores in a plasmolyzed condition.

Helicodendron tubulosum appears to be a stage in the complicated life history of *Clathrosphaera spirifera* described by Zalewski,[2] a life-history divided into four phases represented by as many spore forms. Through the kindness of Professor Wiener of Harvard, the writer was enabled to obtain a full translation of this paper, and from a study of this to draw the following conclusions. In the first place, the four spore forms,—the clathroid spores, the helical spores, a sclerotium-like stage for which he adopts the name "spore complex," and a clustered oidium-like type of fructification,—occurred from early spring to late fall in the sequence given. Zalewski complained of the frequent contaminations of his cultures by *Penicillium*, and even though he noticed the resemblance of his "spore complexes" to the sclerotia that so frequently are produced by that ubiquitous fungus, he seemed willing to concede such a stage to his new genus without attempting to isolate it and carry it through its life history in pure culture. Also, the connections between the other phases were not ascertained by direct observation. During a study of

[1] Cooke, M. C. Grevillea **3**: 178. *pl. 48, fig. 3.* 1875.

[2] Zalewski, A. Rozpraw Spraw. Wydz. matem.-przyr. Akad. Krakau **18**: 153–191. *7 pl.* 1888.

the cultures extending over many months, although two stages were found in the same culture, in no case did Zalewski find one stage actually giving rise to another, thus justifying the conclusion that other fungi in a dormant state were present. Yet because of the resemblance between the content of the spiral and the clathroid spores, because of the similarity between the hyphae of germination of the two forms, it was thought to be a single life history of which these forms were different stages. The only culture that Zalewski carried through a complete cycle of spore forms was a gross culture. This gives added significance to his statement that many cultures kept under the same conditions gave rise to different combinations of spore forms. In any event there must remain some uncertainty as to the true life-cycle of *Clathrosphaera* until it is again collected and the life history studied in pure culture.

Specimens examined:

England: Hereford, *J. G. Morris* (no spores) (K).

Austria: Wienerwald, *von Höhnel* (F).

United States:

Massachusetts: Cambridge, on *Salix* twigs, *Linder* (slide F, L); Arlington, *Martin* (F).

4. **Helicodendron fuscum** (B. & C.) Linder, n. comb.

Helicosporium fuscum Berkeley & Curtis, in Berkeley, Grevillea **3**: 51. 1874.

Helicosporium thysanophorum Ellis & Harkness, Torr. Bot. Club Bull. **8**: 27. 1881.

Helicoon thysanophorum (E. & H.) Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 49. *fig. 16.* 1892.

Plate 27, figs. 5–6.

Colony inconspicuous, densely cespitose or sometimes effuse, "Mummy Brown to "Sepia," under the hand lens "Saccardo's Umber" from masses of spores. Conidiophores very short, erect. Spores subhyaline to dilute brownish, consisting of filaments 1.5–2.5 μ thick, coiled in 3 planes to form 5–12-seriate, cylindrical bodies, 14.4–27 × 10.8–14.4 μ. The spores proliferate to form branching chains.

Specimens examined:

Exsiccati: Ellis, N. Am. Fungi, 552.

United States:

New Jersey: Newfield, *J. B. Ellis*, type of *Helicosporium thysanophorum*, in Ellis, N. Am. Fungi.

South Carolina: *Curtis*, TYPE (K, slide F).

5. Helicodendron hyalinum Linder, n. sp.

Plate 27, figs. 3–4.

Colonies white, scattered, minute, the dried material visible only under the low power of the microscope. Conidiophores hyaline, ascending, sparsely branched, 15–40 × 1.3–2 μ. Conidia hyaline, the filament 1.2–1.75 μ thick, coiled in 3 planes to form short, 2–5-seriate, cylindrical spore bodies 11 × 8–10 μ.

On decaying wood.

This species, on account of the few-seriate, small, hyaline spores, is quite distinct from any species heretofore described.

Specimens examined:

United States:

Massachusetts: Waverley, on decaying wood, Oct. 12, 1899, *R. Thaxter*, TYPE (F); under wet boards, Oct. 1, 1892, *R. Thaxter* (F); South Billerica, *Clinton* (F).

HELICOSTILBE

Helicostilbe von Höhnel, emended.

Helicostilbe von Höhnel, Kön. Akad. Wiss. Wien, math.-nat. Kl. Sitzungsber. **111**: 1028–1029. 1902.

The type species is *Helicostilbe simplex.*

Conidiophores aggregated to form a stele. The conidia acrogenous, in terminal clusters, not produced on scandent or repent mycelium, non-hygroscopic, similar to those of *Helicoma.*

Thus emended, *Helicostilbe helicinum* is excluded from this genus and transferred to *Helicomyces,* as explained in the discussion under *Helicomyces scandens.* The genus is represented by a single species.

1. **Helicostilbe simplex** Petch, Roy. Bot. Gard. Peradeniya, Ann. **7**: 321. 1922.

Plate 28, figs. 10–12.

Synnemata scattered, up to 0.8 mm. high and 30 μ in diameter, black, equal, slightly spreading at the base, each arising from a small attachment disc of coalescent hyphae, the stalk glabrous, at least in small specimens, the hyphal elements fuscous, terminating in slightly swollen club-shaped apices which may be simple or branched, erect or recurved. The conidia acrogenous, solitary, fuliginous, 1–1¼-times coiled, 3–4-septate, the septa subhyaline, bordered on either side by narrow dark bands, the filaments 4 μ thick, slightly tapering or bluntly rounded at the basal end, bluntly rounded at the distal end; diameter of coiled conidia 8–10 μ.

On the under surface of living leaves of *Daphniphyllum glaucescens.* Ceylon.

In his original description, Petch states that the stalks are villous, with short hyphal tips but in the type material, kindly loaned to the writer by the Curator of the Herbarium of the Royal Botanic Garden in Peradeniya, the stalks were entirely glabrous except for a short distance below the apices. It is possible that the villous appearance is due to fallen spores that have adhered to the stalks. The measurements of the synnemata are those given by Petch.

Specimen examined:

Ceylon: Hakgala, April, 1917, *Petch,* TYPE (Pe 6263, K, and slide F, MBG).

TROPOSPORELLA

Troposporella Karsten, Hedwigia **31**: 299. 1892.

The type and only species is *Troposporella fumosa.*

Sporodochia pulvinate to subspherical, the surface dry, granular, fuliginous to olivaceous. The conidiophores are somewhat branched, closely aggregated, strongly constricted at the septa, light fuscous. Conidia as in *Helicoma.*

This genus appears to be intermediate between species of *Helicoma,* represented by *H. monilipes* and *H. olivaceum,* and *Everhartia.* It differs from the former in that the conidiophores

are very closely aggregated to form a definite and compact subglobose fruiting body; from the latter by the fact that the fruiting body is apparently less highly developed and lacks the gelatinous secretions which make the fruiting bodies of *Everhartia* hard and corneous when dry.

1. **Troposporella fumosa** Karsten, *l.c.*

Plate 29, figs. 10–14.

Sporodochia scattered, pulvinate to subspherical, the surface granular, "Snuff Brown," 200–350 μ in diameter. Conidiophores densely aggregate, sparsely branched, deeply constricted at the septa so as to give a monilioid appearance, dilute to light fuscous, 50–90 × 3–5 μ, the terminal cells when sterile frequently globose and reaching 7 μ in diameter. Conidia dilute to light fuscous, 9–13-septate, the filament closely coiled 1½–2 times, 4–4.5 μ thick, tapering to the truncate basal end, abruptly rounded at the distal end; diameter of coiled conidia 12–16 μ.

On old bark of *Populus* sp. Finland.

The type material of this species was kindly loaned for examination by Dr. Harold Lindberg, to whom the writer wishes to express his deep appreciation.

Specimen examined:
Finland: Mustiala, *Karsten*, TYPE (H, slide F, MBG).

EVERHARTIA

Everhartia Saccardo & Ellis, in Saccardo, Michelia **2**: 580. 1880; Saccardo, Syll. Fung. **4**: 729. 1888; Thaxter, Bot. Gaz. **16**: 204–205. *pl. 20, fig. 10–12.* 1891.

The type species of the genus is *Everhartia hymenuloides.*

Sporodochia verruciform, stipitate to substipitate, superficial, scattered, small. Conidia hyaline or light-colored, surrounded by mucus, flat, tightly coiled 1–2½ times, the filament 3– many-septate, non-hygroscopic.

Everhartia, so far as is known from collections, appears to be confined to temperate North America. The distribution, in the light of present-day knowledge, serves somewhat to delimit the genus. There are, however, other characters which definitely

separate this genus from the tropical *Delortia* into which von Höhnel transferred *E. lignitalis*. In the first place, the fruiting bodies of *Everhartia* do not appear to be as large or as gelatinous as those of *Delortia*. On drying, the species of *Everhartia* become corneous, and, although shrinking, apparently retain somewhat of their original shape. The other genus, although often as much as one centimeter in diameter, dries down until nothing remains but a flat, somewhat glazed layer on the substratum. This behavior is due to the fact that relatively few sterile threads, much exceeding the length of the conidiophores, secrete a copious supply of mucilaginous material in which the spores are imbedded. In *Everhartia* the conidiophores, while having a mucilaginous sheath, are much more numerous and aggregate to form a definite sporodochial body of almost parallel threads which maintain the shape of the fruiting body after it is dry. In addition, the spores are definitely produced on the outside of the fructification. Such conspicuous differences in the fruiting body alone are sufficient to separate the two genera.

KEY TO THE SPECIES OF EVERHARTIA

1. Conidia 3-septate..*1. E. lignitalis*
1. Conidia more than 3-septate..2
2. Conidia 4–8-septate..*2. E. candida*
2. Conidia more than 8-septate..*3. E hymenuloides*

1. **Everhartia lignitalis** Thaxter, Bot. Gaz. **16**: 204–205. *pl. 20, fig. 10–12*. 1891.

Delortia lignitalis (Thaxt.) von Höhnel, Kön. Akad. Wiss. Wien, math.-nat. Kl. Sitzungsber. **125**: 89–90. 1916.

Plate 29, figs. 1–4.

Sporodochia scattered, superficial, stipitate or substipitate, yellowish, becoming blackish towards the base, subcylindrical or expanding upwards, 250–400 × 100–150 μ. Spores hyaline, terminal, 3-septate, *the filament* 3.5–4 μ in diameter, the rounded base and snout-like apex approaching one another in a single convolution 12–13 *(8–10)* × 7–9 μ; extruded in a yellow viscous rounded mass. Sporiferous hyphae septate, subdichotomously branched, mingled with longer, usually simple, sterile hyphae.

The above is the original description with the writer's modifications in italics.

On wet decaying wood. Eastern United States.

Specimens examined:

United States:

Connecticut: West Haven, on wet logs, *Thaxter*, TYPE (F).
Tennessee: Burbank, Aug. 1896, *Thaxter* (F).

2. Everhartia candida Thaxter in herb. n. sp.

Plate 29, figs. 5–7.

Sporodochia scattered, superficial, irregularly hemispherical or elongate, 0.5–1 × 0.5–2 mm., white, when dry yellowish and horny. Conidia hyaline, disc-shaped, coiled 1½–1¾ times, 4–7-septate, imbedded in mucus; the conidial filament 3–3.5 μ thick, bluntly rounded at the distal end, tapering to a narrow truncate basal end; the coiled conidia 9–12 μ in diameter. Sterile hyphae hyaline, slender, mostly confined to the periphery of the sporogenous area.

On decaying wood. Eastern United States.

Specimens examined:

United States:

Maine: York, Aug. 14, 1897, Sept. 22, 1892, *Thaxter* (F); Kittery Point, Aug. 30, 1890, *Thaxter*, TYPE (F).
New Hampshire: Intervale, Sept. 1901, *Thaxter* (F).
Maryland: Corunna, July, 1891, *Thaxter* (F).

3. Everhartia hymenuloides Saccardo & Ellis, in Saccardo, Michelia **2**: 580. 1880.

Plate 29, figs. 8–9.

Sporodochia sessile, irregular in shape, dark fuscous, scattered, small, horny when dry. Conidia hyaline or dilute colored, coiled 2–2½ times, 16–25-septate, imbedded in a yellow-olive mucus; the conidial filament 2.5–3.5 μ thick, abruptly rounded at both ends; diameter of coiled conidia 13–18–(20) μ.

On *Sorghum nutans*. New Jersey.

Von Höhnel mentions finding microconidia in old colonies. These he states measure 3 × 1.6 μ, and are found in the slime.

He also questions the status of the species, stating that because of its gelatinous texture and the greenish slime, it should be considered an alga.

Specimens examined:

Exsiccati: Ellis, N. Am. Fungi, 969.

United States:

New Jersey: Newfield, *Ellis, 3582,* TYPE, in Ellis, N. Am. Fungi.

DELORTIA

Delortia Patouillard, in Patouillard & Gaillard, Soc. Myc. Fr. Bull. **4**: 43–44. *pl. 13, fig. 5 a–f.* 1888; Saccardo, Syll. Fung. **6**: 795. 1888.

The type species of the genus is *Delortia palmicola.*

Sporodochia tuberculiform, gelatinous, white. Spores 1–3-septate, hyaline, coiled in 2 planes, non-hygroscopic. The conidiophores slender, hyaline, septate, abruptly swollen below the conidia. Sterile hyphae exceeding the conidiophores, long, slender, flexuous, secreting a copious supply of mucilaginous material which serves as a matrix. One species.

1. Delortia palmicola Patouillard, *l.c.*

Plate 29, figs. 19–23.

Sporodochia tuberculiform, milky-gelatinous, up to 1 cm. in diameter, composed of hyaline, septate, branched mycelium; the vegetative parts and conidia imbedded in a gelatinous matrix. Conidiophores slender, 1.2–2.5 μ in diameter, sparsely branched, swollen at the apex to form an apophysis-like structure 3–3.5 μ thick. Conidia hyaline, 2–4-septate, the filament once-coiled to form horse-shoe-shaped body 17.5–21–(25) μ diam.; the filament 13–14 μ thick, abruptly rounded at the distal end, bluntly tapering-rounded at the basal end.

On decaying parts of palms, more rarely on other decaying wood. Tropical America, Liberia.

Although considered to belong to the Tremellaceae by Patouillard, there is little evidence for so classifying this species unless the gelatinous character is given undue importance. From

an examination of material preserved in formaldehyde, swollen in lacto-phenol, and then stained with Delafield's hematoxylin, it is clear that nuclear behavior does not substantiate such a position. The nucleus in the terminal cell of the conidiophore enlarges and then divides, one daughter nucleus migrating to the conidium initial, the other remaining in the now-swollen cell of the conidiophore where it apparently disintegrates with the remainder of the cell content when the conidium reaches maturity (pl. 29, fig. 19 a–d). In the conidium, the nucleus migrates to the center of the cell and there divides, following which the first septum is laid down. The further history and behavior of the nucleus was impossible to learn because of the improperly killed material. It is clear, however, that the intervals in laying down the septa are very irregular, and that the procedure does not follow that of the Auriculariales, to say nothing of the Tremellales.

Specimens examined:

Grenada: *Thaxter* (F).

Venezuela: Atures, *Gaillard*, TYPE (F).

British Guiana: Bartica, *Linder, 722;* Koreai Creek, Essequibo River, on decaying *Cecropia* wood, *Linder, 721;* Plantation Vryheid, Demerara River, *Linder, 920* (F).

Liberia: Firestone Plantation No. 3, Du River, *Linder* (F).

HOBSONIA

Hobsonia Berkeley, in Massee, Ann. Bot. **5**: 509. *1 fig.* 1891; Saccardo, Syll. Fung. **11**: 653. 1895.

The type species is *Hobsonia gigaspora.*

Sporodochia verruciform, gelatinous or dry and granular on the surface. Conidia of long stout filaments, multiseptate, coiled in 3 planes or irregularly to form tangled knots, often proliferating.

This species appears to be closely allied to *Delortia.* The spores of the genus, however, are irregularly coiled, multiseptate, and often proliferating, while those of *Delortia* are constantly flat, few-septate, and never proliferate. These characters are sufficiently distinct to warrant the separation of the two genera. *Hobsonia* is represented by two species.

1. **Hobsonia gigaspora** Berkeley, *l.c.*
Hobsonia Ackermanni Patouillard, Soc. Myc. Fr. Bull. **18**: 185. *1 fig.* 1902.

Plate 28, figs. 6–9.

Sporodochia milky-white, gelatinous when fresh, "Cinnamon Buff" and horny in the dried state. The conidiophores hyaline, branched, slender, 1.8–3 μ thick, imbedded in the gelatinous matrix. Conidia spirally or irregularly coiled, at maturity forming tangled knots, the filament hyaline, multiseptate, (6)–8–12–(14) μ thick, often proliferating.

On dead wood. West Indies and northern South America.

Patouillard, in describing his species, states that it differs conspicuously from *H. gigaspora* by the dimensions of the receptacle and the form of the spore. The spores of *H. Ackermanni* as shown in the figure are equally as typical of *H. gigaspora,* and the sizes obtained from type material intergrade so that it is impossible to separate the two species on this character. The receptacle, or apex of the conidiophore, upon which Patouillard laid so much stress is found to be the same as that in typical *H. gigaspora.* Other diagnostic characters for separating these two species are lacking.

Specimens examined:

Dominica: *W. R. Elliott, 379, 452, 1441,* as *Helicomyces mirabilis* (BM); ex herb. Massee (NY).
Guadeloupe: *Ackermann,* type of *H. Ackermanni* (F).
Grenada: Grand Etang, *Thaxter* (F).
Trinidad: Aripo Savannah, *Thaxter* (F).
Venezuela: (F, K) TYPE.

2. **Hobsonia mirabilis** (Peck) Linder, n. comb.
Helicomyces mirabilis Peck, N. Y. State Mus. Rept. **34**: 46. *fig. 6–10.* 1881.

Plate 28, figs. 1–5; pl. 31, fig. 1.

Colonies as white tufts or irregular patches, 200 μ or more in diameter, not gelatinous or if gelatinous not conspicuously so, drying to "Ochraceous Buff," the surface powdery or granular. Conidiophores hyaline, slender, 1.5–3 μ thick, branched, septate,

surrounded below by gelatinous sheaths, but not imbedded in a gelatinous matrix. Conidia at first spirally coiled to form a more or less conical spore body, later irregularly coiled to produce tangled knots, the filaments hyaline, multiseptate, (9)–12–15–(17) μ thick, proliferating.

On decaying plant remains. Eastern United States.

The type of this species was collected in Ithaca, New York, by Prentiss and sent to Peck who described this species, and it is probably in the herbarium of the New York State Museum, Albany, New York.

Hobsonia mirabilis differs from *H. gigaspora* in the non-gelatinous colonies, a character apparently not due to seasonal variations in humidity, since the latter species when collected in Trinidad during the dry season was even then gelatinous, according to Dr. Thaxter's field notes. There are also other characters that separate the two species. The conidiophores of *H. gigaspora* are subdichotomously branched, at least near the conidia, while those of this species appear to be less frequently branched; the conidiophores at the base of the conidia are spirally coiled in the younger stages of *H. gigaspora*, and not at all or only slightly so in this species. The conidia also show some slight differences, the width of the spore filaments as measured across the septa being greater in this species. This is shown in the accompanying graph (fig. 16) where the spores of the gelatinous species are represented by approximately an equal number of *H. gigaspora* and *H. Ackermanni*. It shows clearly the difference in the sizes of the gelatinous and non-gelatinous species. In addition the spores have a more turgid appearance and the protoplasmic content is denser.

Specimens examined:

United States:

New York: Ithaca, *Dudley* (F).

Tennessee: Burbank, on corn cob and stems of *Aristolochia* sp., Aug. 10, 1896, *Thaxter* (F).

DREPANOCONIS

Drepanoconis Schroeter & Hennings, Hedwigia **35**: 211. 1896; Saccardo, Syll. Fung. **14**: 457. 1899.

Clinoconidium Patouillard, Soc. Myc. Fr. Bull. **14:** 156. 1898.

The type species is *Drepanoconis larvaeformis.*

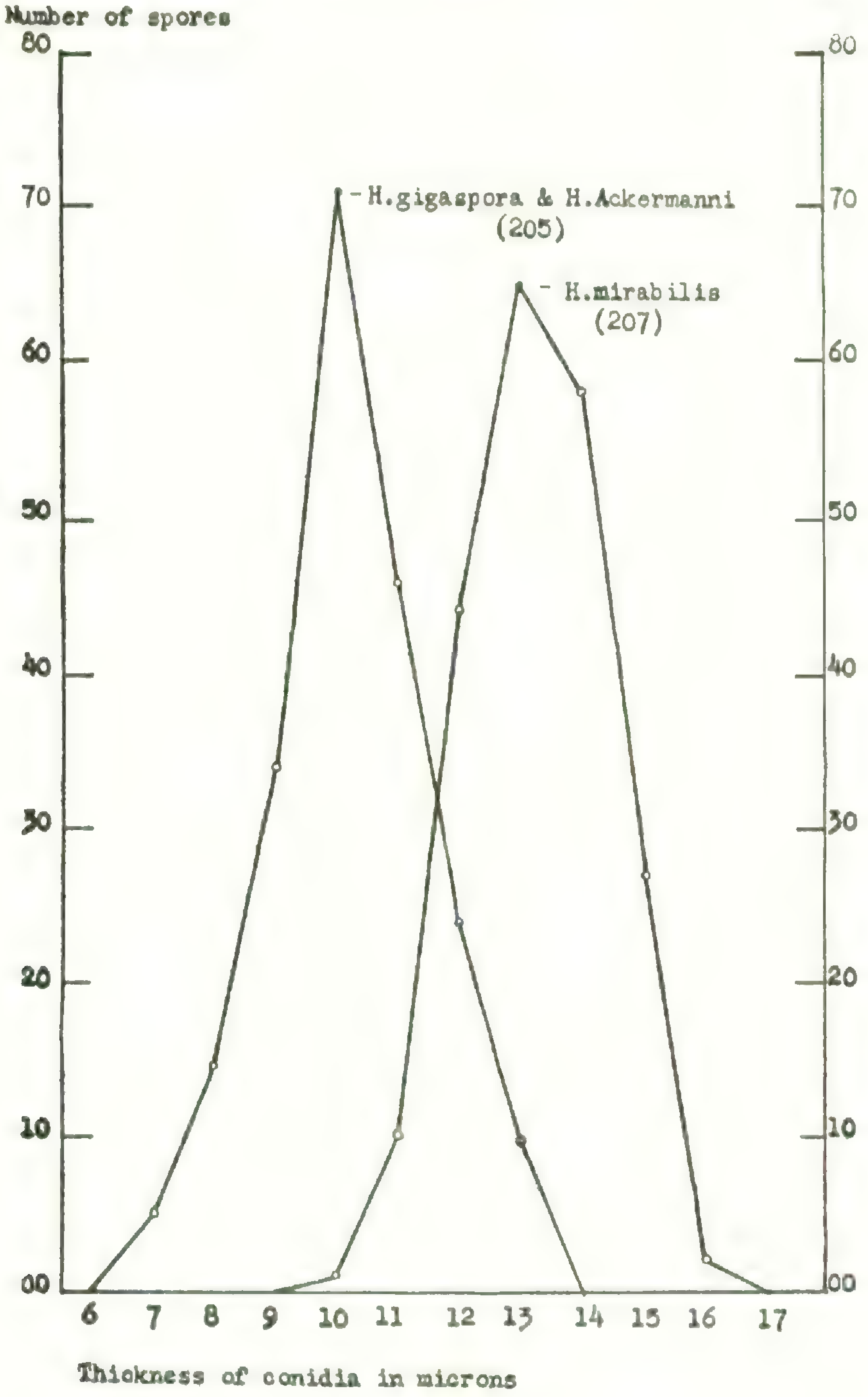


Fig. 16.

Sterile mycelium intercellular, forming a layer under the epidermis of the host, at first covered, then erumpent. The conidiophores hyaline, short, erect, simple, between the longer

and more slender, erect, flexuous, sterile hyphae. The conidia ¾–1½-times coiled, the filament thick, non-hygroscopic, the cell wall thick, often laminated in appearance, the cell content occupying approximately one-third the width of the filament.

The spores of this genus are thoroughly characteristic and serve to identify it even when the pseudostromatic nature of the mycelium is not clearly observed. The sterile hyphae are often crowded with the freed spores, under which condition they appear to be conidiophores, although a section of the material clearly demonstrates their sterility. The genus is represented by two species, both of which are probably parasitic.

1. **Drepanoconis larvaeformis** Spegazzini, Mus. Nac. Buenos Aires, Ann. **9**: 9. 1903.

Helicomyces larvaeformis Spegazzini, Fungi Guar. **1**: 158. 1883.

Drepanoconis brasiliense Schroeter & Hennings, in Hennings, Hedwigia **35**: 211. 1896.

Uredo farinosa Hennings, Hedwigia **36**: 216. 1897.

Clinoconidium farinosum (Henn.) Patouillard, Soc. Myc. Fr. Bull. **14**: 156. 1898.

Drepanoconis fructigena Rick, Ann. Myc. **3**: 17. 1905.

Marsonia fructigena Rick, not Bresadola, Broteria **5**: 53. *pl. 5, fig. 10.* 1906.

Plate 29, figs. 15–17.

Colonies when fresh are white, on drying become "Light Buff" to light "Ochraceous Orange," at first subcutaneous, then erumpent, producing a pulvinate thickening when growing on leaves. Sterile mycelium intercellular, forming a mat from which arise the sterile hyphae and the conidiophores. Sterile hyphae hyaline, flexuous, simple or sparingly branched, 1–1.5 × 162–235 μ, much exceeding the conidiophores. Conidiophores hyaline, simple or occasionally branched above, 2–3 × 30 μ. Conidia acrogenous, hyaline, ½–1-coiled, soon deciduous, 4–9-celled, the cells in a single row, 2.5–4.5 μ thick, surrounded by a thick, hyaline, lamellate wall, making the diameter of the filament 10–17 μ; the coiled spore 16–24 μ in diameter.

Growing on fruit and leaves of Lauraceae. South America.

This species, although described in the Uredinales and Peronosporales, has found its place among the Fungi Imperfecti where it is to be hoped that it will remain. It is quite distinct from the related species, *D. anguisporus*. The uniseriate arrangement of the cells, the irregular horse-shoe shape, and the smaller size characterize it. *Drepanoconis fructigena* was said by Rick to differ from the accepted species by its smaller spores. Measurements of a large series of spores from the type of that species clearly indicate that although the spores vary somewhat in size, they intergrade with, and are essentially the same as, those of *D. larvaeformis*.

Judging by the following quotation from Rick's account in 'Broteria' of *Marsonia fructigena*, the species is parasitic. He says, "Die befallenen Früchte schwellen stark an und bekommen eine rötliche gefelderte Oberhaut. Schliesslich wird letztere abgeworfen und es erscheint der weisse, mehlige Ueberzug."

Specimens examined:

Exsiccati: Balansa, Plant. Uruguay., 3758.

Brazil: Sao Leopoldo, on fruit of *Oreodaphnis*, *Rick, 42*, type of *D. fructigena* (F); on leaves of *Nectandra* (F).

Uruguay: Guarapi, on fruit of Lauraceae, *Balansa*, in Plant. Uruguay., TYPE.

2. **Drepanoconis anguisporus** (Pat. & Lagerh.) Linder, n. comb.
Helicomyces anguisporus Patouillard & Lagerheim, in Patouillard, Soc. Myc. Fr. Bull. **8:** 137. *pl. 12, fig. 4.* 1892.

Plate 29, fig. 18.

Mycelium cespitose, innate, later erumpent, effuse, pulverulent, white. Sterile hyphae flexuous, 100–200 × 1.8–3 μ, free above, the apex often slightly inflated. Conidia subsessile, produced in great number, hyaline, horse-shoe shaped, flat or spirally twisted, 1–1½-times coiled, the distal end slightly tapering, bluntly rounded, the basal end bluntly tapering-rounded to a broad, truncate apiculus 2–2.5 μ in diameter, 5–13-times septate, the protoplasmic content of the spore uniseriate or irregularly 2-seriate, the filament 9–18 μ thick; the coiled spore 21–41.5 μ in diameter.

Growing on the fruit of Lauraceae. Ecuador.

Specimen examined:
Ecuador: Pallatanga, *Lagerheim*, TYPE (B, F).

TROPOSPORIUM

Troposporium Harkness, Cal. Acad. Sci. Bull. **1**: 39. 1884; Morgan, Cinci. Soc. Nat. Hist. Jour. **15**: 52. 1892.

The type species is *Troposporium album.*

"Sporodochium superficial, verruciform, farinaceous; hyphae long, slender, flexuous, branched, the spores borne at the apex of slender branchlets. Spores spirally coiled into an elongate ellipsoidal body. The spores are like those of *Helicoon.*"

This genus is the only one in the Tuberculariaceae that has the spores coiled in 3 planes as in *Helicoon.* There is only one species, the type of which has been lost.

1. Troposporium album Harkness, *l.c.*

"Sporodochium white, verruciform, thick, often confluent; hyphae slender, flexuous, branched, hyaline, the spores borne at the ends of slender branchlets. Spores hyaline, oblong-ellipsoidal, composed of 3–7 spires, closely coiled; spore 40–45 × 18–22 mic.; the thread about 7 mic. in thickness, continuous.

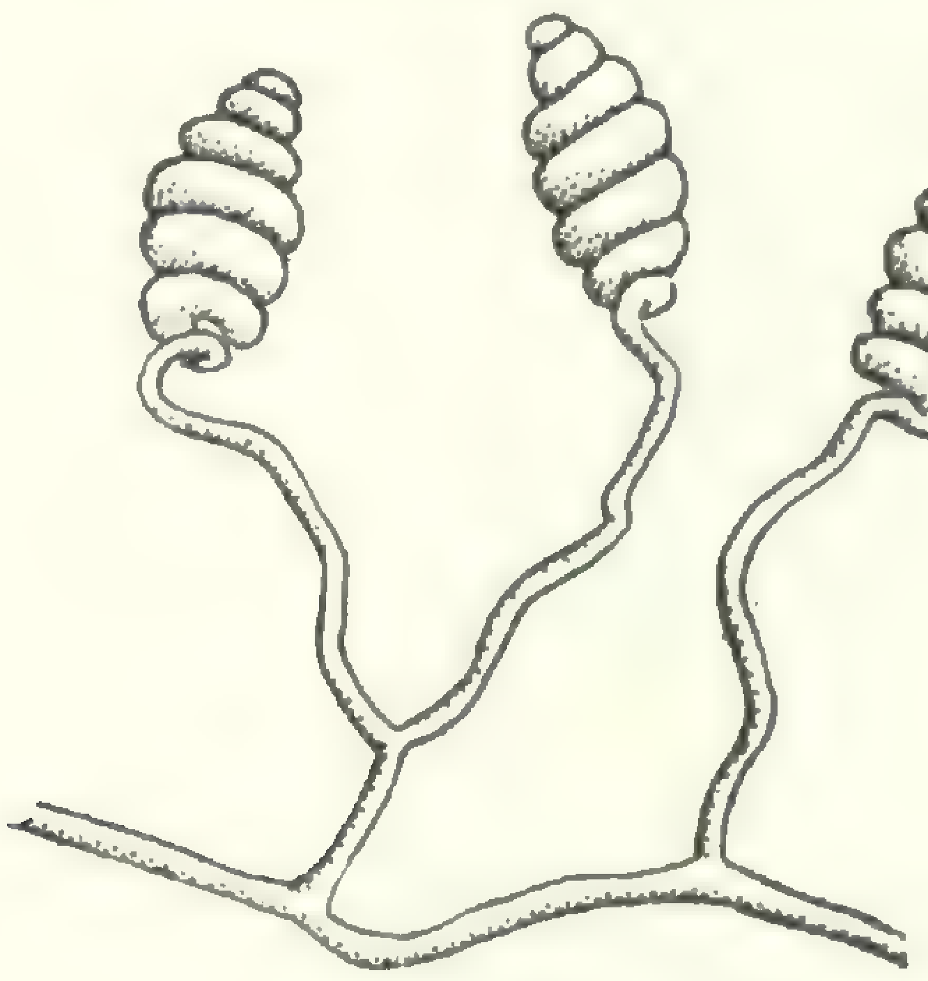


Fig. 17. *Troposporium album.* After Morgan.

"Growing on dead stems of *Corylus rostrata.* California. Harkness.

"The stroma consists of numerous granules and oil globules which are set free by breaking."

The above descriptions of the genus and species are taken from Morgan's monographic study of the North American Helicosporeae (*l.c.*).

INDEX TO SPECIES IN PART II

New scientific names and combinations are printed in **bold face** type; synonyms in *italics*; and previously published names, in ordinary type.

	Page
Acanthostigmella	
genuflexa	288
Thaxteri	321
Byssosphaeria helicophila	320
Chaetosphaera parvicapsa	322
Clathrosphaeria	331
Clinoconidium	342
farinosum	343
Delortia	338
lignitalis	336
palmicola	338
Drepanoconis	341
anguisporus	344
brasiliense	343
fructigena	343
larvaeformis	343
Everhartia	335
candida	337
hymenuloides	337
lignitalis	336
Gyroceras nymphaearum	294
Helicodendron	329
fuscum	332
hyalinum	333
paradoxum	329
triglitziensis	330
tubulosum	330
Helicodesmus	329
albus	330
Helicoma	295
ambiens	310
ambiguum	273
asperothecum	311
atroseptatum	307
bambusae	319
Berkeleyi	304, 318
binale	318
binale var. *apertum*	318
candidum	316
conicodentatum	311
Curtisii	312
fasciculatum	315
griseum	285
intermedium	306
larvale	322
limpidum	301
microscopicum	299
minutissimum	298
monilipes	302
Morgani	304
Mülleri	307
olivaceum	302
palmigenum	306
perelegans	303
phaeosporium	304
polysporum	300
proliferens	309
recurvum	312
repens	300
roseolum	297
simplex	315
stigmateum	298
velutinum	305
violaceum	303
Helicoma	317
Helicomyces	270
albus	271, 275
ambiguus	273
anguisporus	344
aureus	279
bellus	273
brunneolus	308
candidus	316
cinereus	282
clarus	271
Curtisii	313
diplosporus	319
elegans	271
fasciculatus	315
fuscus	288
gracilis	281
larvaeformis	343
microscopicus	299
mirabilis	340
Mülleri	308
niveus	298

Page

olivaceus ... 277
roseus ... 271
scandens ... 274
sphaeropsidis ... 298
tenuis ... 272
triglitziensis ... 330
tubulosus ... 330
vegetus ... 277
Helicoon ... 322
auratum ... 325
ellipticum ... 326
Fairmani ... 325
farinosum ... 324
fuscosporum ... 326
politulum ... 328
reticulatum ... 327
Richonis ... 323
sessile ... 325
thysanophorum ... 332
tubulosum ... 331
Helicopsis ... 295
olivaceus ... 302
punctata ... 302
Helicoryne ... 295
ramosa ... 327
viride ... 307
Helicosporium ... 275
albidum ... 287
albo-carneum ... 290
ambiens ... 310
auratum ... 325
aureum ... 279
Berkeleyi ... 318
binale ... 319
Boydii ... 305
brunneolum ... 308
brunneum ... 291
cinereum ... 282
Curtisii ... 312
decumbens ... 284
diplosporum ... 319
Elinorae ... 290
ellipticum ... 327
Ellisii ... 291
fasciculatum ... 315
Fuckelii ... 277
fuscum ... 332
gracile ... 281
griseum ... 285

Page

griseum ... 282
guianensis ... 280
herbarum ... 292
intermedium ... 306
intermedium var. *palmigenum* ... 306
leptosporum ... 282
limpidum ... 301
lumbricoides ... 282
lumbricoides ... 282
lumbricopsis ... 284
microscopicum ... 299
monilipes ... 302
Mülleri ... 307
nematosporum ... 288
nymphaearum ... 294
olivaceum ... 277
pallidum ... 286
phaeosporium ... 304
phragmites ... 287
pilosum ... 279
politulum ... 328
polysporum ... 300
populi ... 293
prasinum ... 293
pulvinatum ... 293
pulvinatum var. *effusum* ... 277
ramosum ... 327
recurvum ... 312
repens ... 300
Richonis ... 323
serpentinum ... 288
simplex ... 315
spectabile ... 304
thysanophorum ... 332
Tiliae ... 313
vegetum ... 277
velutinum ... 305
viride ... 308
Helicostilbe ... 333
helicina ... 274
simplex ... 334
Helicostilbe ... 333
Helicotrichum ... 276
albo-carneum ... 290
brunneum ... 291
candidum ... 316
populi ... 293
pulvinatum ... 277, 293
Herpotrichia pezizula ... 314

	Page
Hobsonia	339
Ackermanni	340
gigaspora	340
mirabilis	340
Lasiosphaeria	
Elinorae	290
nematospora	289
pezizula	314
Lituaria stigmatea	298
Marsonia fructigena	343
Melanomma helicophilum	320
Sphaeria	
helicoma	229
helicophila	320
pezizula	314
Troposporella	334
fumosa	335
Troposporium	345
album	345
Uredo farinosa	343
Xenosporella	317
Berkeleyi	318
larvalis	322
pleurococca	318
Thaxteri	320

Explanation of Plate

PLATE 12

Fig. 1. *Helicomyces scandens* Morgan

A specimen in the intermediate stage of development, showing the loosely fasciculate, hyaline conidiophores clustered about the dark sterile setae. The transition from hyaline hyphae to the dark, pointed, sterile portions of the setae is clearly shown. × 500.

Fig. 2. *Helicomyces scandens* Morgan

An early stage of development of the fungus, previous to the formation of fascicles and the accompanying setae. × 500.

Fig. 3. *Helicomyces scandens* Morgan

A rudimentary seta produced in culture on potato dextrose agar. × 500.

Fig. 4. *Helicomyces scandens* Morgan

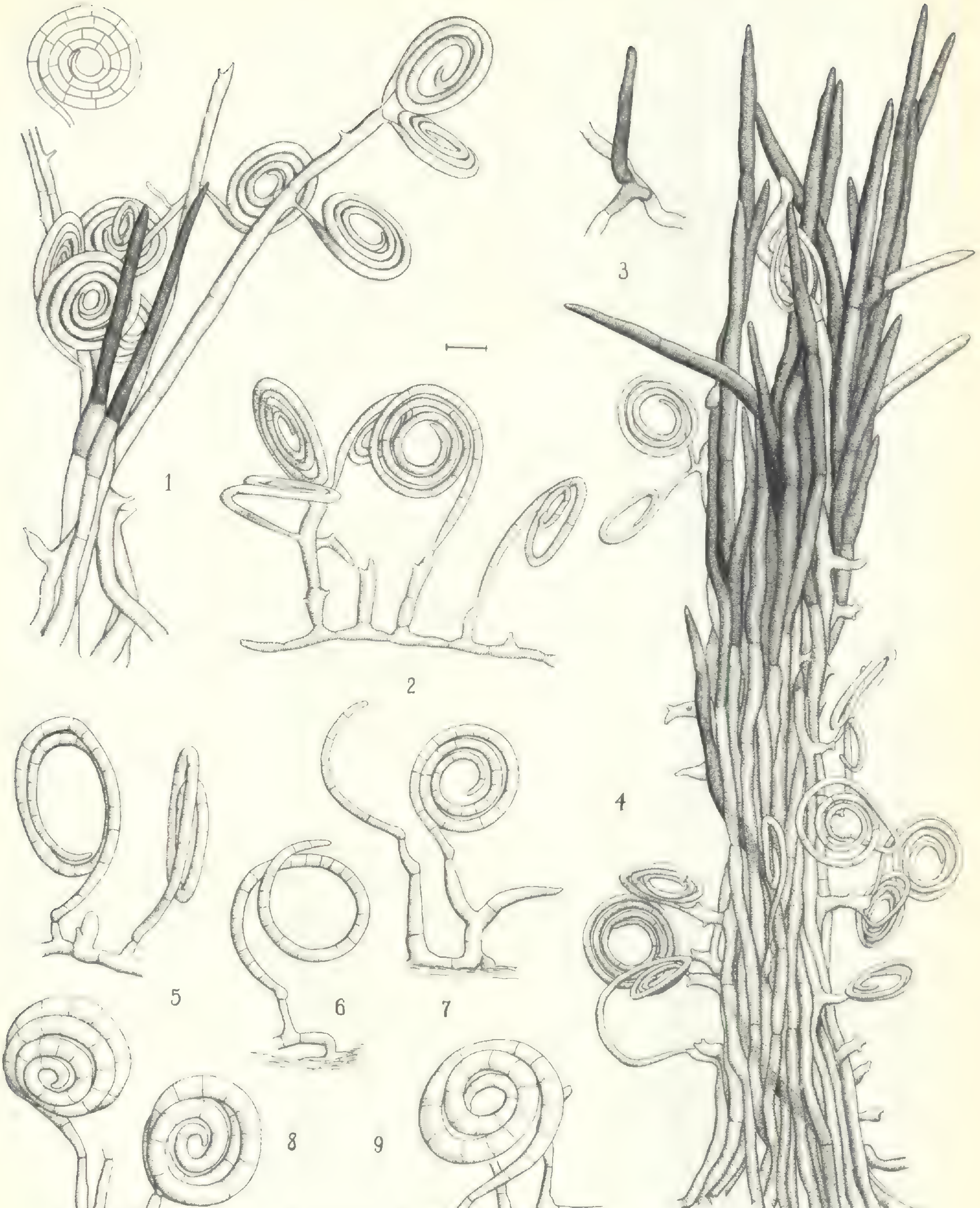
A fully mature specimen in which the sporogenous hyphae are fasciculate and the setae are numerous. × 500.

Figs. 5–7. *Helicomyces roseus* Lk.

The conidia are borne obliquely, either directly on the repent mycelium or else on short, ascending branches. × 500.

Figs. 8–9. *Helicomyces ambiguus* (Morgan) Linder

The stout conidia, coiled in 3 planes, are shown attached directly to the conidiophore, not obliquely as in *H. roseus*. Drawings made from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 13

Figs. 1–2. *Helicosporium vegetum* Nees

Young material that shows the simple erect conidiophore bearing the conidia on minute cylindrical teeth. Such young material has passed under the name of *H. olivaceum* Morgan. Fig. 2 is a drawing made from German material (*von Höhnel*, Wienerwald, June 9, 1907). × 500.

Fig. 3. *Helicosporium vegetum* Nees

A mature specimen in which the spores, in addition to being produced on the erect conidiophores, are also borne on a simple, elongate, subhyaline, lateral branch. Drawing from Missouri material (*Linder*, Gray Summit, MBG 66538). × 500.

Fig. 4. *Helicosporium gracile* (Morgan) Linder

A portion of a scandent, pellucid, fertile hypha that has given rise to simple conidiophores. Drawing from Iowa material (*G. W. Martin*). × 500.

Fig. 5. *Helicosporium guianensis* Linder

A mature specimen that shows the characteristically branched, bladder-like sporogenous projections. Drawing from type material. × 500.

Fig. 6. *Helicosporium guianensis* Linder

Less-mature specimens in which the bladder-like projections are simple. The terminal cells of the conidiophores are occasionally slightly inflated. Drawing from type material. × 500.

Fig. 7. *Helicosporium gracile* (Morgan) Linder

Erect conidiophores that have arisen from repent sterile mycelium. × 500.

LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 14

Fig. 1. *Helicosporium aureum* (Cda.) Linder

The dark, erect, bristle-like conidiophores are shown with the lateral hyaline, bladder-like projections that bear 2 or more sporogenous teeth. The conidiophore on the left is more mature and has begun to branch in the manner characteristic of the species. × 500.

Fig. 2. *Helicosporium aureum* (Cda.) Linder

A slightly higher magnification of one of the bladder-like projections.

Fig. 3. *Helicosporium aureum* (Cda.) Linder

A secondary, fuscous, ovoid conidium formed on the terminal portion of an erect conidiophore. Slightly above and on the opposite side may be seen a projection from which a similar spore has fallen. From material growing on bark. × 500.

Fig. 4. *Helicosporium aureum* (Cda.) Linder

A germinating spore. × 1145.

Figs. 5–6. *Helicosporium aureum* (Cda.) Linder

Early stages in the formation of the dark perithecium-like bodies. From van Tieghem cell culture. × 500.

Fig. 7. *Helicosporium aureum* (Cda.) Linder

A spore which, swelling in preparation for germination, has ruptured its yellow exospore. × 1145.

Fig. 8. *Helicosporium aureum* (Cda.) Linder

Penetration of the substratum by a vegetative hypha. × 500.

Fig. 9. *Helicosporium gracile* (Morgan) Linder

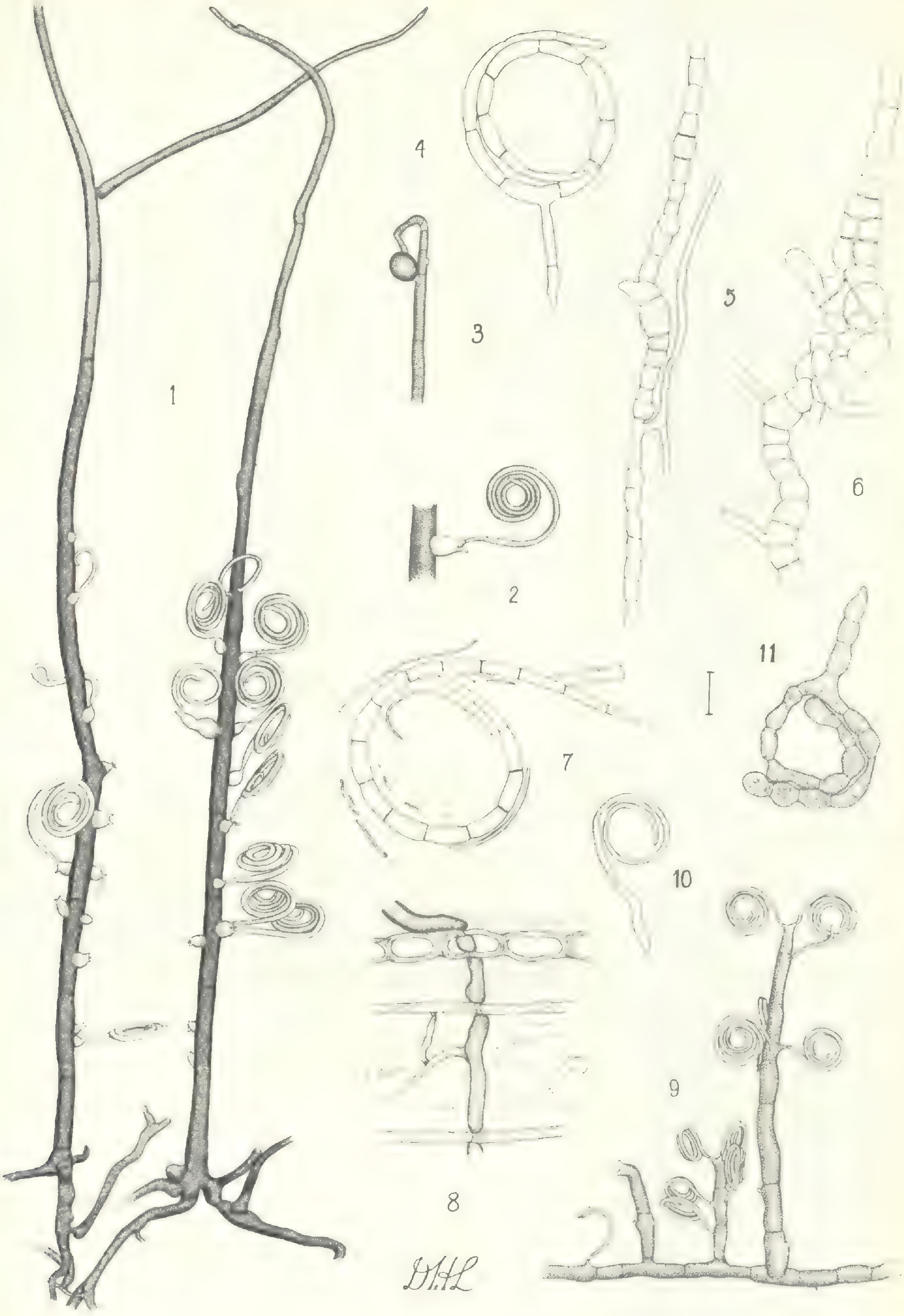
Upright conidiophores that arise from the creeping fertile hyphae. × 500.

Fig. 10. *Helicosporium gracile* (Morgan) Linder

A spore germinating by the elongation of the terminal cell, a method characteristic of this species. × 500.

Fig. 11. *Helicosporium gracile* (Morgan) Linder

The germination of a spore after one month at 98.9 per cent relative humidity. Note the dark color and the bulging cell walls. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 15

Figs. 1–2. *Helicosporium decumbens* Linder

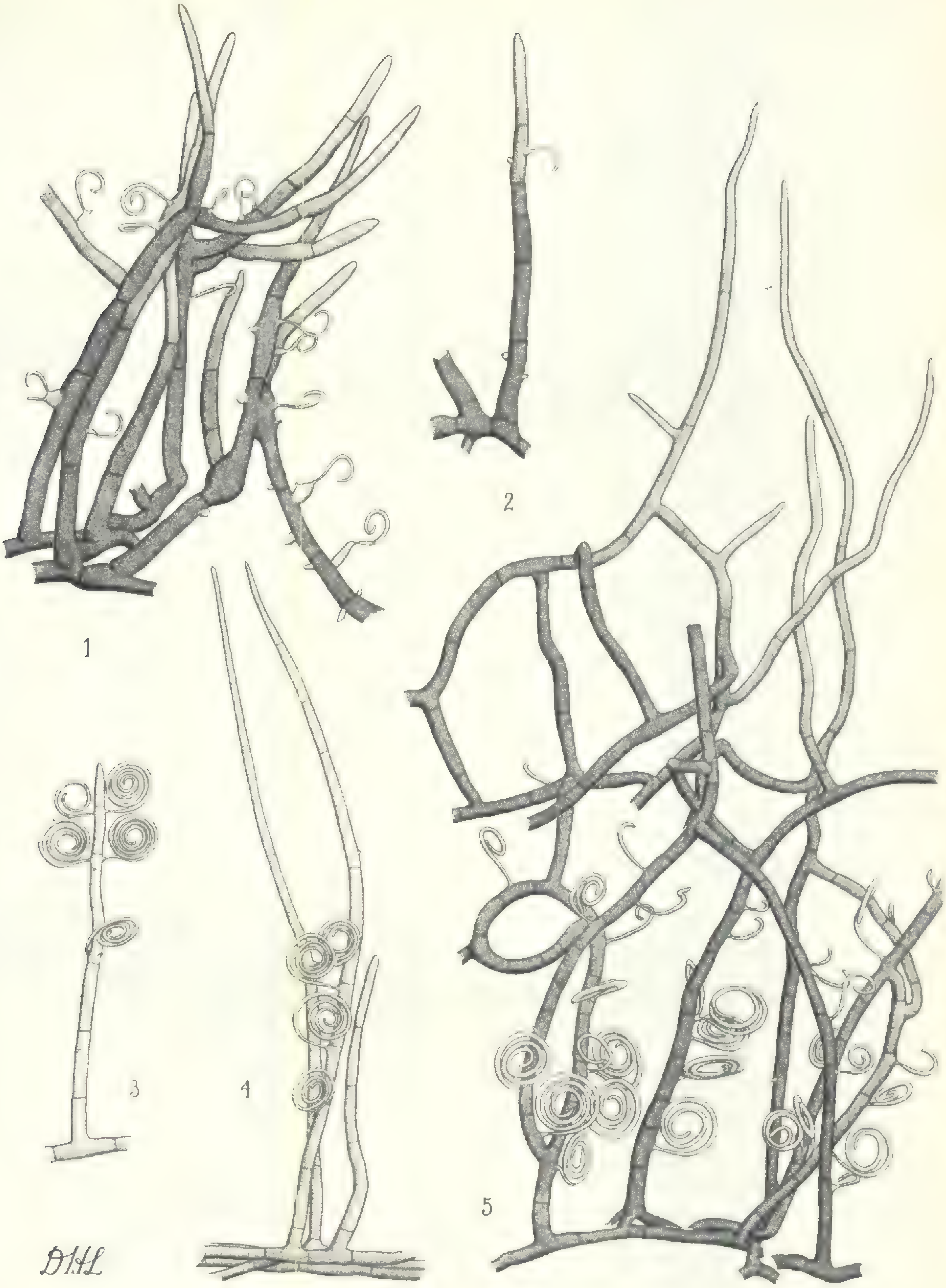
Conidiophores and conidia. The conidiophores are rather short, slightly bulging occasionally, and almost horizontally branched above in the older material. The conidia are produced either on simple minute teeth or else on inflated, bladder-like lateral projections of the conidiophores. Drawings from type material. × 500.

Figs. 3–4. *Helicosporium griseum* (Bonorden) Saccardo

Drawing from material collected by von Höhnel (Austria, Wienerwald). × 500.

Fig. 5. *Helicosporium lumbricoides* Saccardo emend. Matruchot

The conidiophores of this material are typically much branched and repeatedly anastomosed. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 16

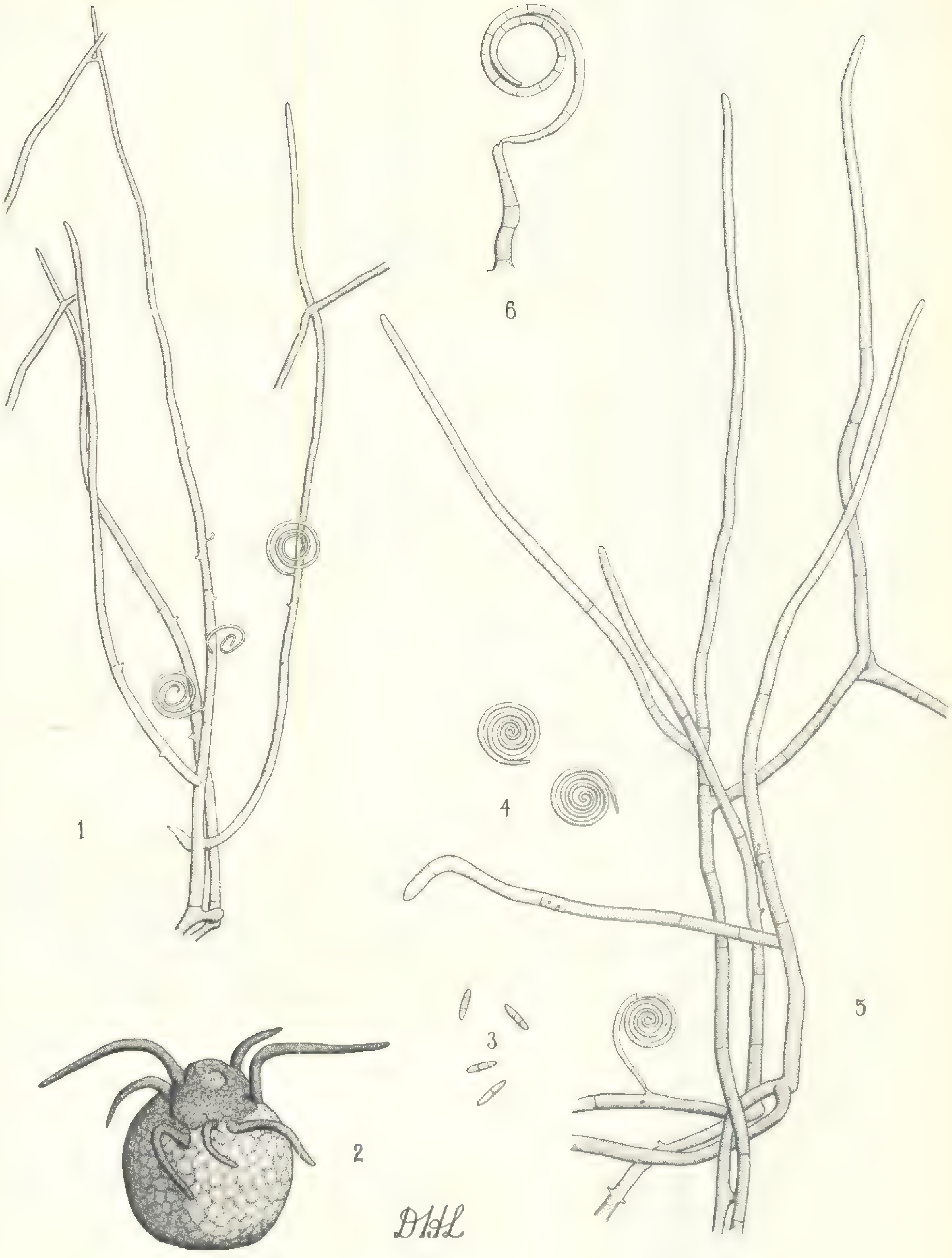
Fig. 1. *Helicosporium pallidum* Ces.
The upper parts of the conidiophores have anastomosed with adjacent ones of the same species. Drawings from type material. × 500.

Fig. 2. *Acanthostigmella genuflexa* von Höhnel
The perithecial stage of *Helicosporium phragmites* with its characteristic curved bristles below the ostiole. Drawing from type material. × 275.

Fig. 3. *Acanthostigmella genuflexa* von Höhnel
Ascospores from type material. × 500.

Figs. 4–5. *Helicosporium phragmites* von Höhnel
The conidiophores of this species are stouter, more loosely branching, and more frequently septate than are those of *H. pallidum*. Drawings from type material. × 500.

Fig. 6. *Helicosporium lumbricopsis* Linder
An immature specimen that has not become branched. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

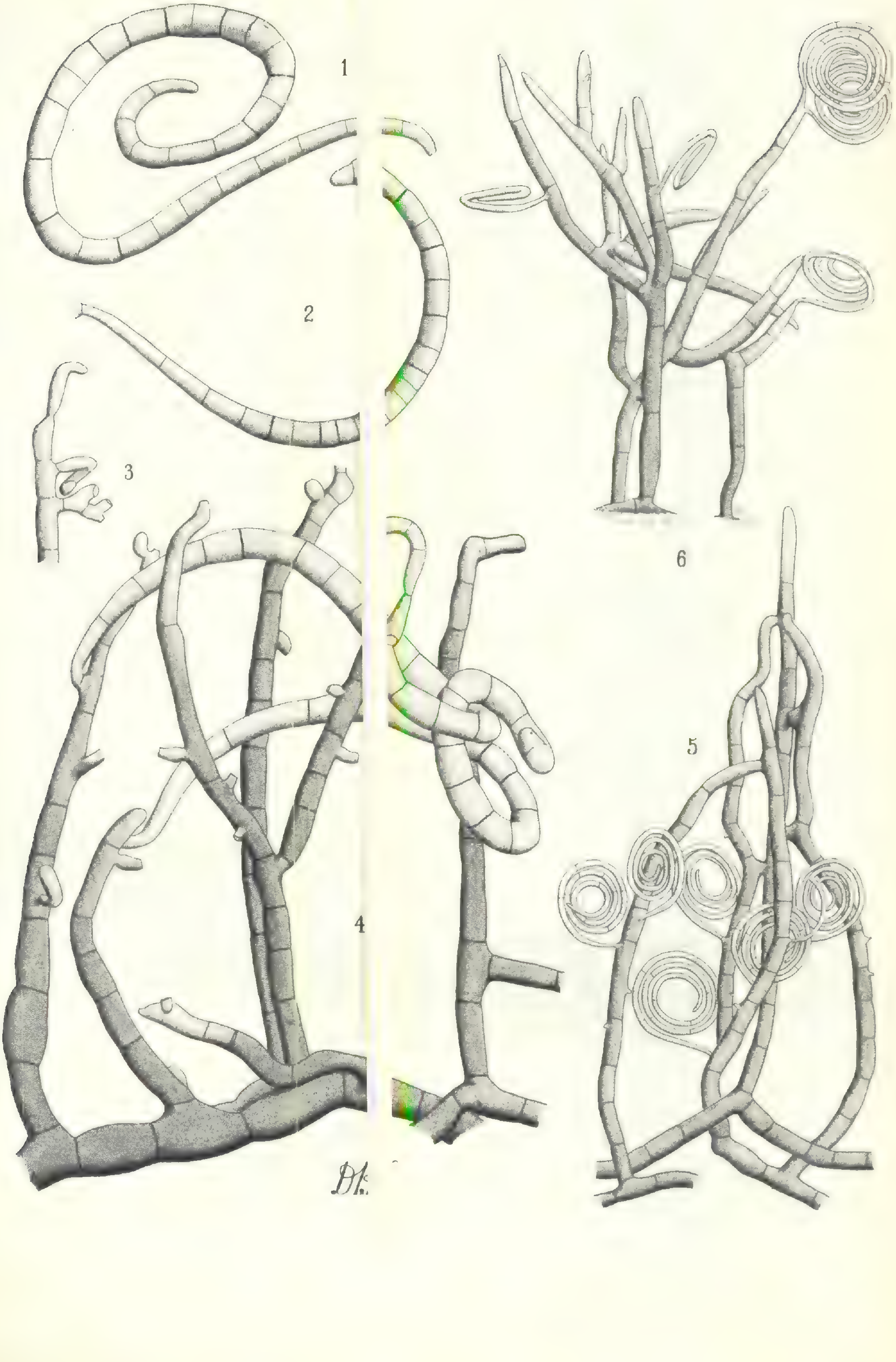
PLATE 17

Figs. 1–2. *Helicosporium serpentinum* Linder
Two immature conidia. Drawings from type material. × 500.

Fig. 3. *Helicosporium serpentinum* Linder
Tip of a conidiophore showing the stout sporogenous teeth and 2 very immature conidia. Drawing from type material. × 500.

Fig. 4. *Helicosporium serpentinum* Linder
Conidiophores with 2 mature conidia. Drawing from type material. × 500.

Figs. 5–6. *Helicosporium lumbricopsis* Linder
The two figures illustrate different types of branching, both of which may be present in the same colony. Fig. 5 drawn from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 18

Fig. 1. *Helicosporium nematosporum* Linder
A characteristic specimen from temperate regions (*Thaxter*, New Haven, Conn.). × 500.

Fig. 2. *Helicosporium nematosporum* Linder
"Sclerotes pedicelées" in association with the above material. × 500.

Fig. 3. *Lasiosphaeria nematospora* Linder
The perfect stage of *Helicosporium nematosporum* and found in connection with that species in the British Guiana material. Drawing from type. × 28.

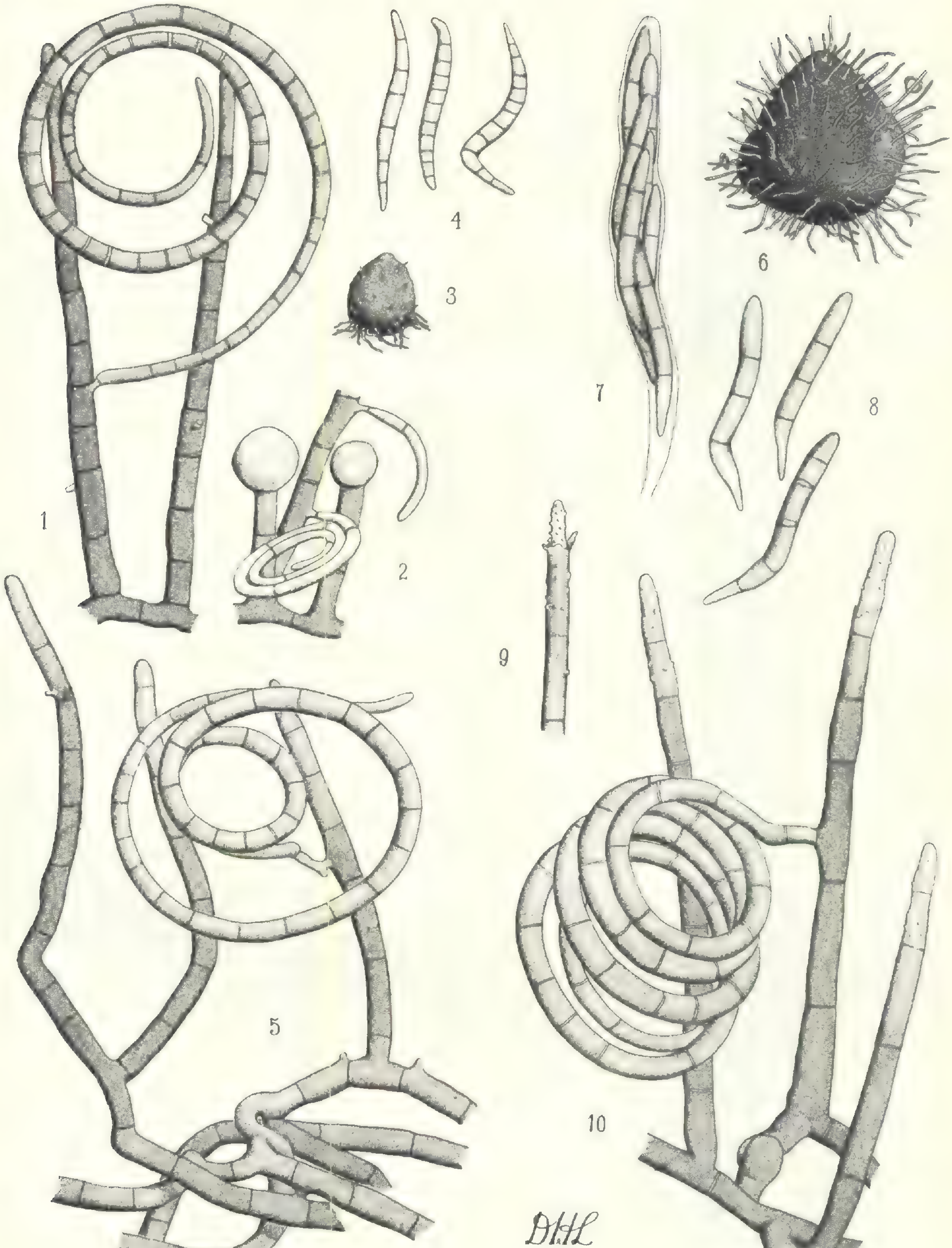
Fig. 4. *Lasiosphaeria nematospora* Linder
Ascospores from type material. × 500.

Fig. 5. *Helicosporium nematosporum* Linder
The conidiophores of this material from British Guiana are more abundant and less stiffly erect in the more developed specimens than are those of temperate specimens. × 500.

Fig. 6. *Lasiosphaeria Elinorae* Linder
The perfect stage of *Helicosporium Elinorae*. Some of the bristles on the perithecium, as is shown, frequently bear conidia. Drawing made from type material. × 28.

Figs. 7–8. *Lasiosphaeria Elinorae* Linder
Ascus and ascospores from the type material. The tapering basal cells of the ascospores are hyaline to subhyaline. × 500.

Figs. 9–10. *Helicosporium Elinorae* Linder
In fig. 9 is shown the end of a conidiophore, of which the colored outer sheath has been ruptured by the hyaline, tuberculate growing point. Fig. 10 illustrates typical conidiophores, of which one bears a dilute fuscous conidium that is coiled in 3 planes. Drawings made from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 19

Fig. 1. *Helicoma roseolum* Thaxter

The hyaline, branched, and anastomosed fertile hyphae are scandent on the dark conidiophores of another Fungus Imperfectus. From type material. × 500.

Figs. 2–3. *Helicoma roseolum* Thaxter

Conidia in optical section. Fig. 3 shows the unique method of attachment of the spores to the conidiophore. From type material. × 500.

Figs. 4–7. *Helicoma minutissimum* Linder

Conidiophores and conidia. Drawings from type material. × 1145.

Fig. 8. *Helicoma minutissimum* Linder

Conidia from type material. × 500.

Figs. 9–10. *Helicoma stigmateum* (Reiss) Linder

Conidiophores and conidia. Drawing from material in Jaap, Fungi Selecti Exsiccati, the type of *Helicomyces niveus*. × 500.

Figs. 11–12. *Helicoma microscopicum* (Ellis) Linder

Drawings from type material. Fig. 11, × 1145; fig. 12, × 500.

Figs. 13–16. *Helicoma olivaceum* (Karsten) Linder

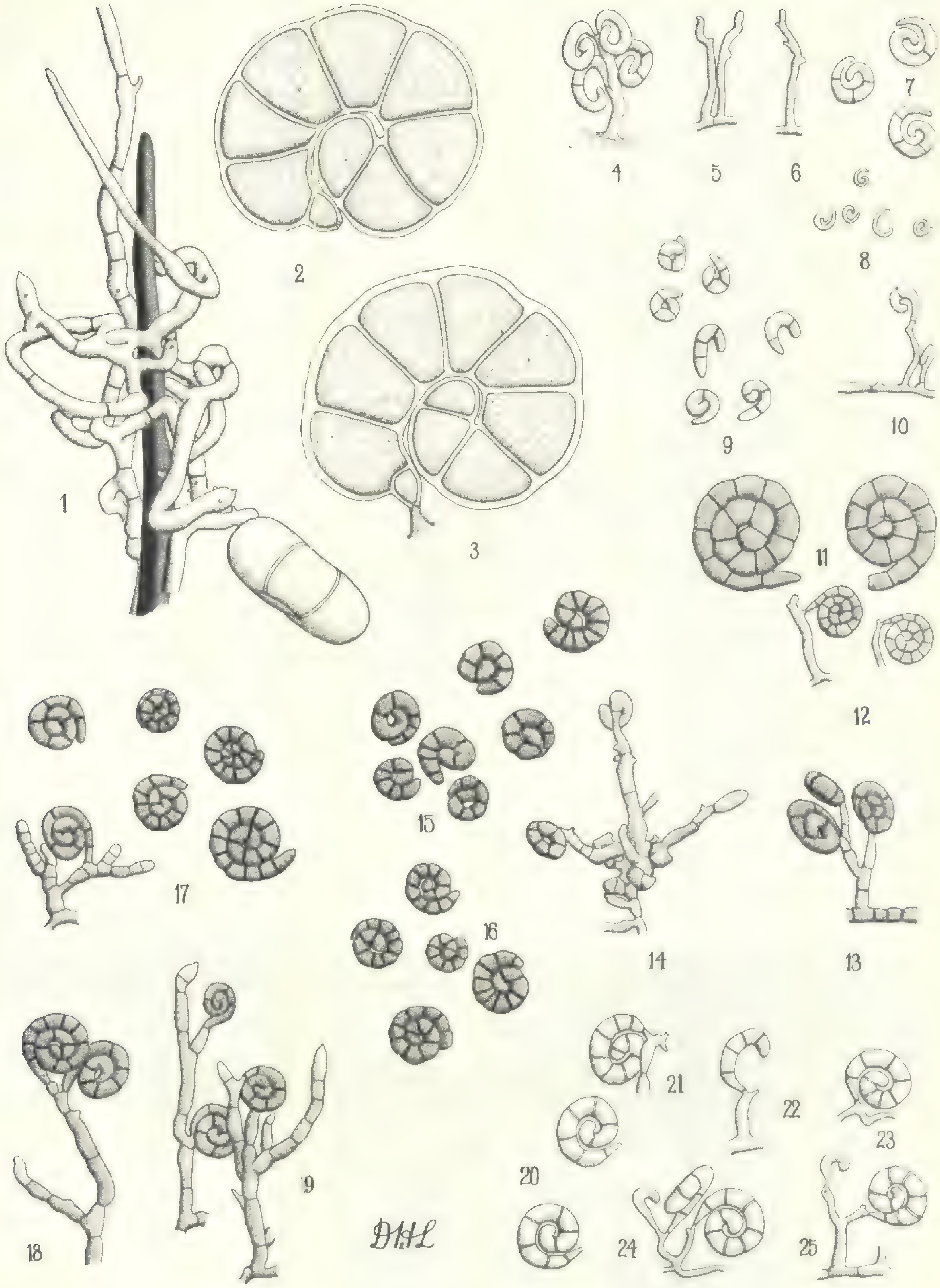
Figs. 13–15 are drawn from the type of *Helicopsis punctata* Pk., and fig. 16 from the type of *Helicopsis olivaceus* Karsten. × 500.

Figs. 17–19. *Helicoma monilipes* Ellis & Johnson

Drawings made from type material. × 500.

Figs. 20–25. *Helicoma polysporum* Morgan

Drawings made from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 20

Figs. 1–2. *Helicoma perelegans* Thaxter

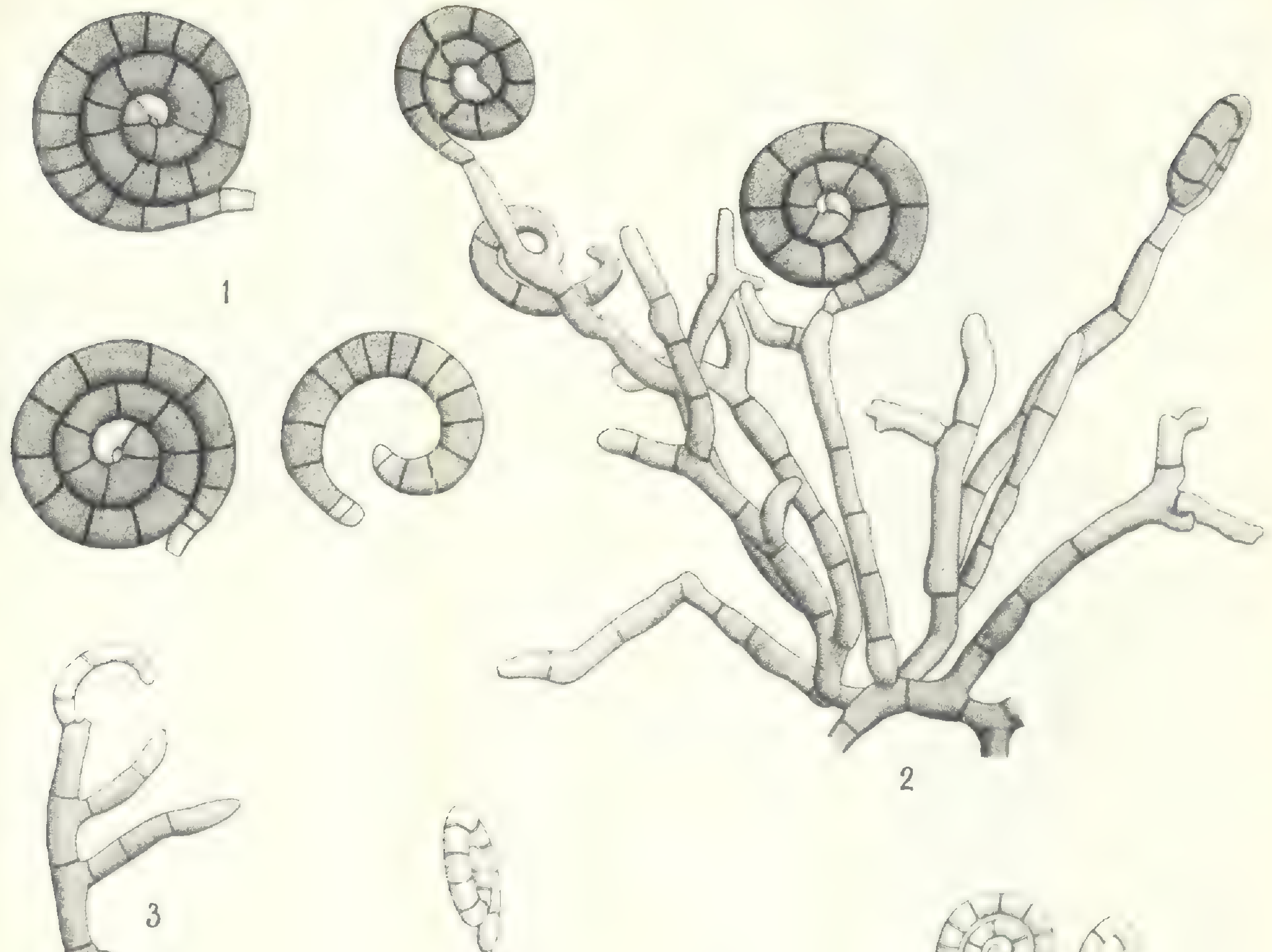
Conidiophores and conidia, the latter with subhyaline terminal cells. Drawings made from type material. × 500.

Figs. 3–5. *Helicoma violaceum* Winter

The conidia are attached obliquely to the conidiophores. Drawings made from type material. × 500.

Fig. 6. *Helicoma Morgani* Linder

Drawing made from type material. × 500.



LINDER--HELICOSPOREAE

Explanation of Plate

PLATE 21

Figs. 1–2. *Lasiosphaeria pezizula* (B. & C.) Saccardo

The gregarious perithecia are the perfect stage of *Helicoma Curtisii.* The still turgid perithecia are surmounted by the white to dilute brown mass of ascospores that has been exuded, while the dried perithecia have collapsed and become cup-shaped. × 28.7.

Figs. 3–4. *Lasiosphaeria pezizula* (B. & C.) Saccardo

Asci showing the thickening of the apices, and the arrangement of the 5–7-septate ascospores within. × 500.

Figs. 5–6. *Lasiosphaeria pezizula* (B. & C.) Saccardo

A single typical mature 7-septate ascospore is shown in fig. 5. Fig. 6 is of an ascospore germinating in a typical fashion by terminal hyphae which are followed by the lateral germ tube. From material in van Tieghem cells. × 500.

Fig. 7. *Helicoma Curtisii* Berkeley

The dark, simple, erect conidiophores are shown bearing single spores on the rounded, tapering apices. The inconspicuous lateral sporogenous teeth should be noted and compared with those of *Helicoma Mülleri.* × 500.

Fig. 8. *Helicoma Curtisii* Berkeley

The end of a conidiophore that has been turned to one side during elongation after the formation of the first spore. × 500.

Figs. 9–10. *Helicoma Curtisii* Berkeley

A conidiophore and conidia from type material. × 500.

Fig. 11. *Helicoma ambiens* Morgan.

Three conidia drawn from co-type material. The slightly stouter filaments and the short, abruptly rounded basal cell distinguish this species from *H. Curtisii.* × 500.

Fig. 12. *Helicoma Mülleri* Corda

The frequently septate conidiophores are shown with their bluntly rounded apices and the stout, pleurogenous, spore-bearing teeth. At *a* is shown a spore that has taken a lateral position as the result of elongation of the terminal cell, and at *b*, a spore-bearing tooth that has become branched. × 500.

Figs. 13–14. *Helicoma Mülleri* Corda

A single cell of a hypha that has turned brown previous to the formation of a conidiophore is shown in fig. 13. Fig. 14 represents a terminal portion of a hyphal branch that has darkened and resembles a conidiophore. From material growing in van Tieghem cells. × 500.

Figs. 15–18. *Helicoma Mülleri* Corda

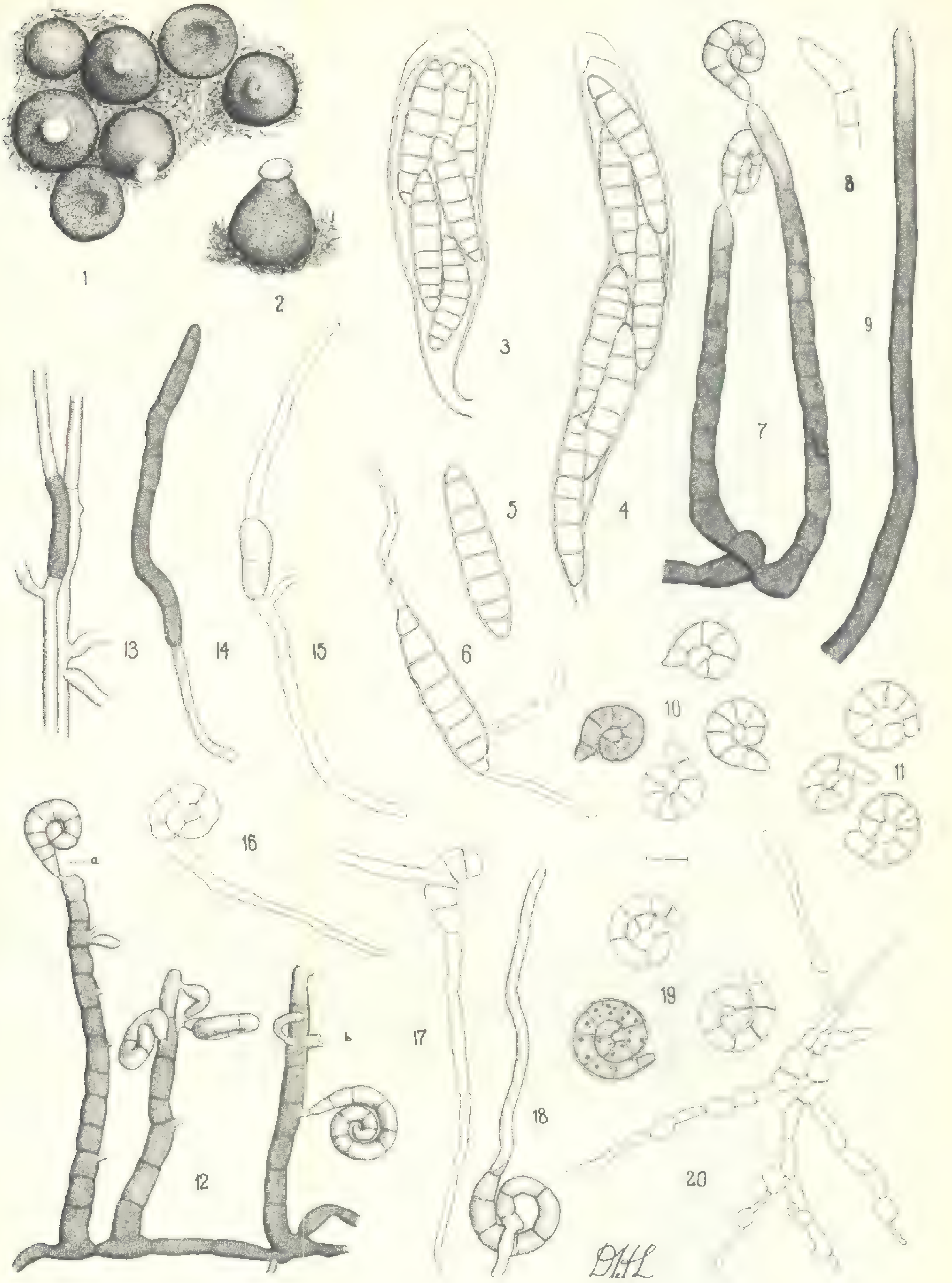
Figs. 15 and 16 are of immature spores that have germinated after having been exposed to freezing temperatures. The latter spore is surrounded by a thick gelatinous sheath. Figs. 16 and 18 demonstrate the germination of conidia by the rupturing of the exospore and the elongation of the basal cell. From material in van Tieghem cell cultures. × 500.

Fig. 19. *Helicoma Mülleri* Corda

A group of spores showing the tapering and truncate basal cells that immediately distinguish this species from *H. Curtisii.* × 500.

Fig. 20. *Helicoma Mülleri* Corda

A conidium that had been germinated at 100 per cent relative humidity and then transferred to 98.9 per cent relative humidity, after which it was allowed to grow for one month. Little growth has taken place, but the cells have become distinctly swollen. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 22

Fig. 1. *Helicoma velutinum* Ellis
Drawings made from co-type material. × 500.

Fig. 2. *Helicoma phaeosporium* Fresenius
Drawings of spores from material collected by the writer at Canton, Mass. × 500.

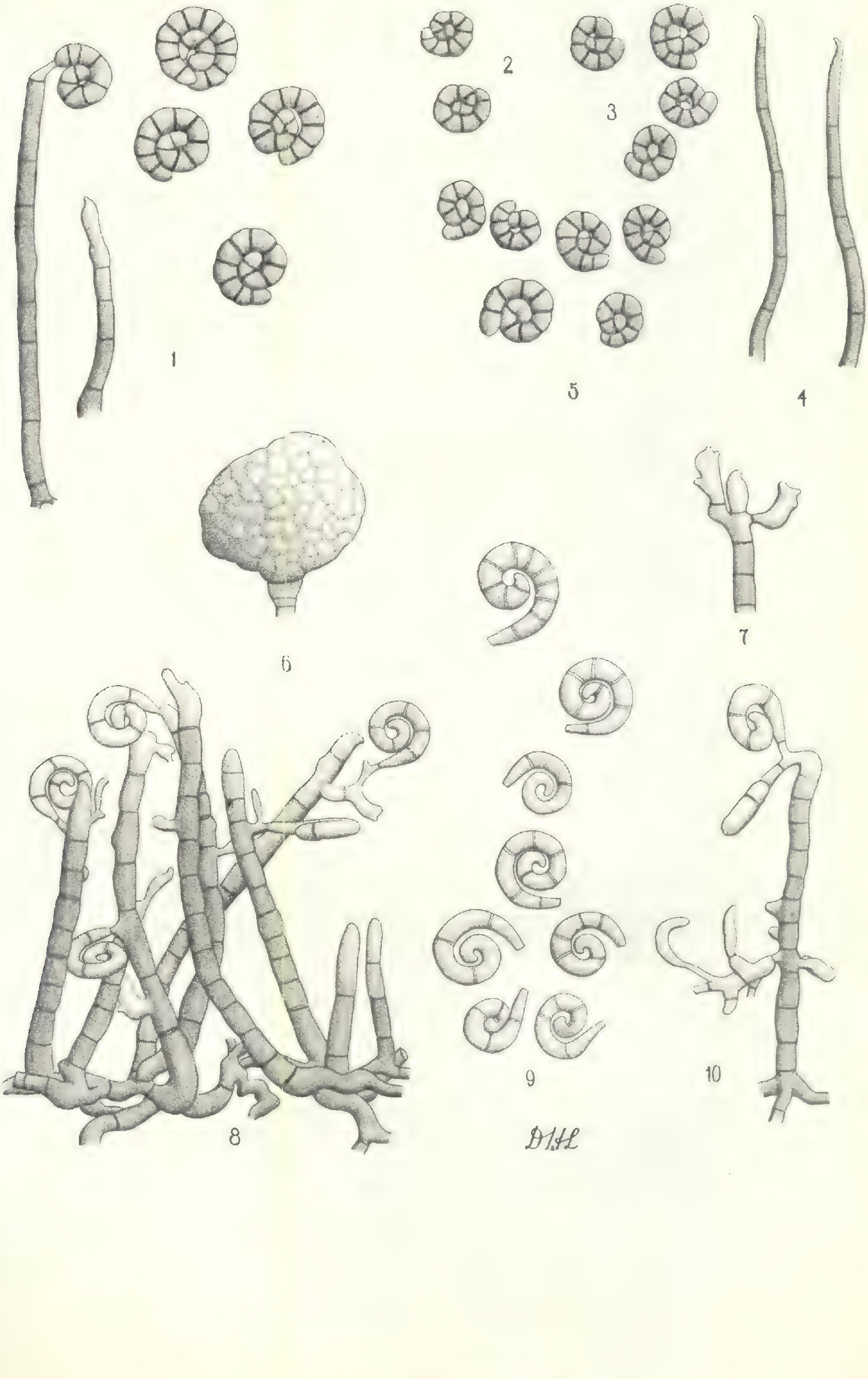
Figs. 3–4. *Helicoma phaeosporium* Fresenius
Drawings made from type of *Helicoma Boydii.* × 500.

Fig. 5. *Helicoma phaeosporium* Fresenius
Drawings made from the type of *Helicoma spectabile.* × 500.

Fig. 6. *Helicoma proliferens* Linder
"Sclerote pedicelée" associated with the conidial stage. From type material. × 500.

Fig. 7. *Helicoma proliferens* Linder
The terminal portion of a conidiophore bearing the stout, proliferating teeth. From type material. × 500.

Figs. 8–10. *Helicoma proliferens* Linder
Conidia and conidiophores. The conidia strongly resemble those of *H. Mülleri* in their tapering truncate basal ends. The conidiophores, however, because of the pronounced proliferation of the sporogenous teeth, are clearly different from those of *H. Mülleri,* as is shown especially clearly in fig. 10. Drawings from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 23

Figs. 1–3. *Helicoma ambiens* Morgan

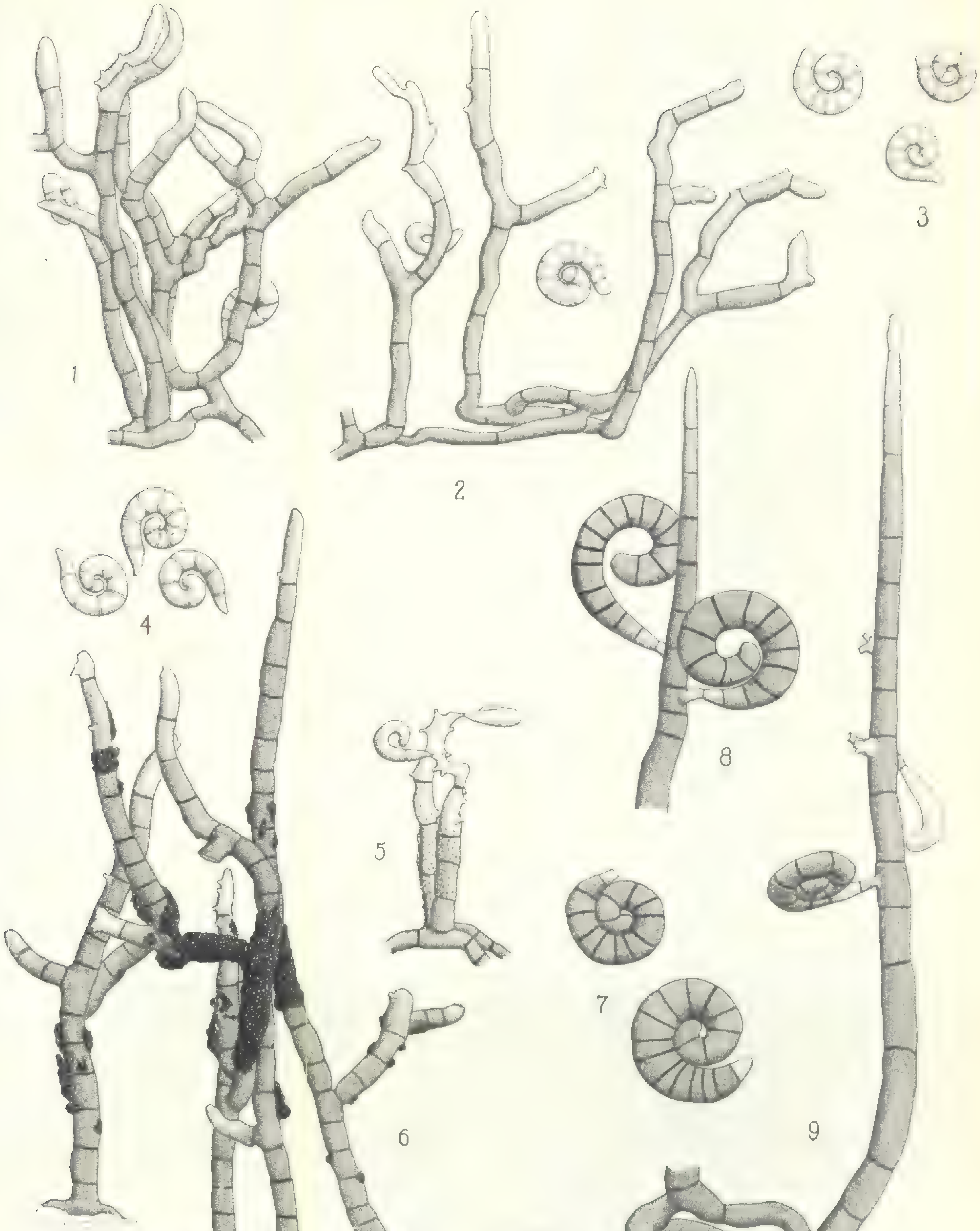
The abruptly rounded and slightly recurved basal ends of the conidia and the conspicuous branching of the conidiophores clearly separate this species from the closely related *H. Curtisii*. Drawings made from co-type material. × 500.

Figs. 4–6. *Helicoma asperothecum* Linder

Conidiophores and conidia. The rough sheath, characteristic of the species, is clearly shown in fig. 5. In the older material, fig. 6, purplish-black secretions are almost invariably present on the conidiophores. Drawings made from type material. × 500.

Figs. 7–9. *Helicoma atroseptatum* Linder

The stout conidia with black septa and subhyaline basal cells, and the simple erect conidiophores characterize this species. Drawings from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 24

Figs. 1–2. *Helicoma simplex* (Sydow) Linder

Conidiophores and conidia. Conidiophores of this species are characterized by the presence of lateral swellings, on which conidia were previously produced. The conidia of this and *H. fasciculatum* are distinct in that at either side of the hyaline septa are distinct dark bands. Drawings from type material. × 500.

Figs. 3–4. *Helicoma fasciculatum* Berkeley & Curtis

The conidia of this species are slightly larger than those of *H. simplex*, and the conidiophores are longer, without the lateral projections. Drawings from type material. × 500.

Figs. 5–6. *Helicoma conicodentatum* Linder

An immature spore-bearing conidiophore is shown in fig. 5. Fig. 6 shows more-mature conidiophores which have commenced to elongate and become scandent. On the subhyaline upper portions of the conidiophores, the conical teeth are clearly in evidence. Drawings from type material. × 500.

Figs. 7–11. *Helicoma recurvum* (Petch) Linder

The stout, tightly coiled conidia, the constrictions in the terminal portions of the conidiophore, and the usual presence of dark crystal deposits separate this species from *H. Curtisii.* Drawings from type material. × 500.

Fig. 12. *Helicoma candidum* (Preuss) Linder

A single conidium from the type material. Compare this with the text figure. × 500.

LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 25

Figs. 1–5. *Xenosporella pleurococca* von Höhnel

The hyaline or subhyaline conidiophores and the subhyaline terminal cells of the conidia mark this as a distinct species. The series of figures illustrate stages in the formation of the mature conidia. Unfortunately, the origin of the peculiar central cell could not be observed. Drawings from type material. × 500.

Figs. 6–11. *Xenosporella Berkeleyi* (Curtis) Linder. All × 500.

Figs. 6, 7. Drawings from type material of *Helicoma Berkeleyi*.

Fig. 8. A single spore from material erroneously identified as *H. velutinum*. (*Langlois*, on dead *Vitis vulpina*, Louisiana).

Fig. 9. Two spores from the type material of *H. diplosporum*.

Fig. 10. Four spores, 2 between figs. 6 and 7, from the type material of *H. bambusae*.

Fig. 11. Conidia and conidiophores from the type material of *H. Berkeleyi*.

Figs. 12–15. *Xenosporella larvalis* (Morgan) Linder

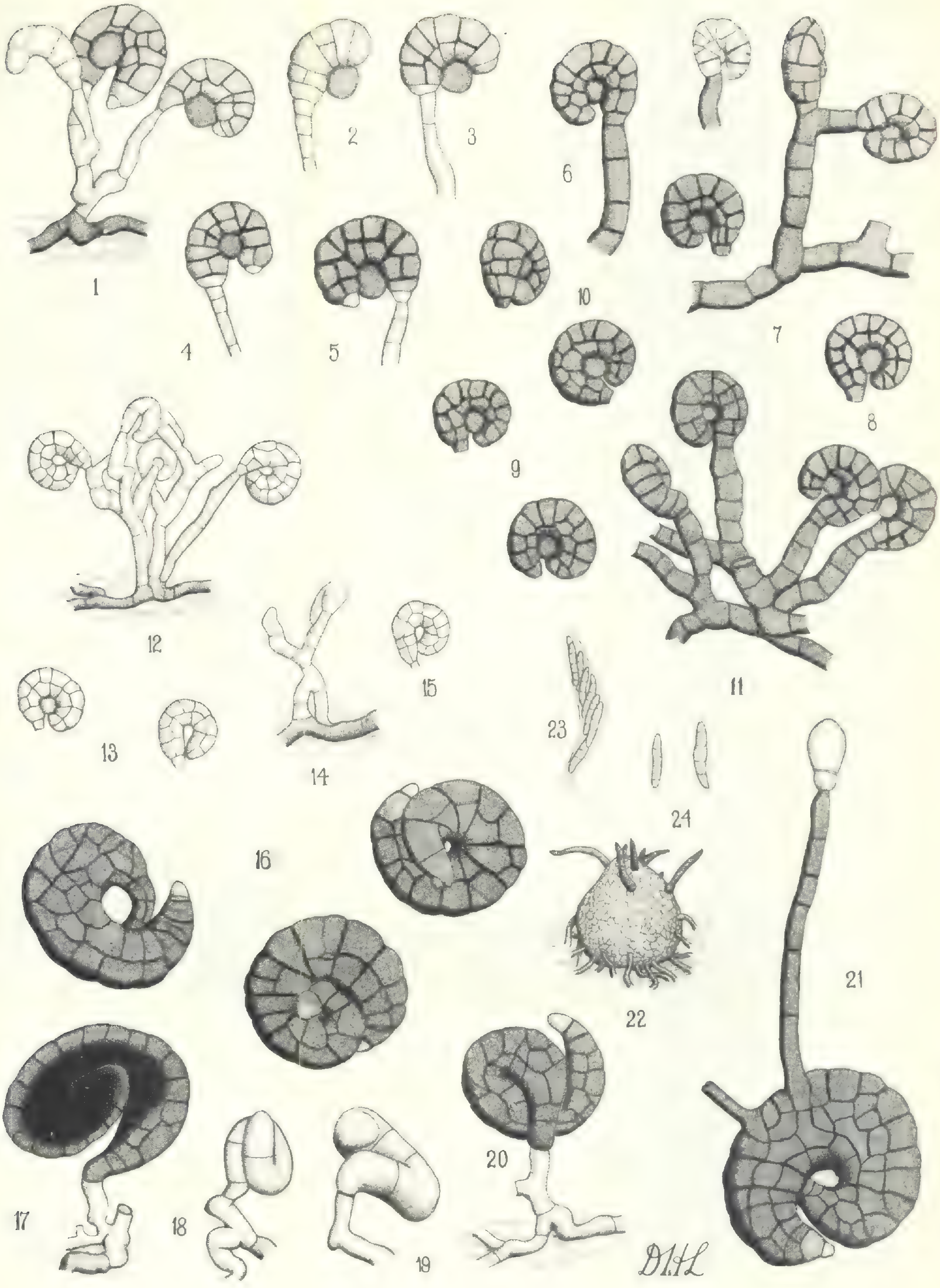
Conidiophores and conidia from type material.

Figs. 16–21. *Xenosporella Thaxteri* Linder

Conidia and conidiophores. The sterile mycelium becomes deep fuscous a short distance from the conidiophores, and when seen under the hand lens is black and glistening. Figs. 18 and 19 show 2 immature conidia, while fig. 21 illustrates a mature conidium giving rise to a secondary spore form. Drawings from type material. × 500.

Figs. 22–24. *Acanthostigmella Thaxteri* Linder

A perithecial stage in association, although not definitely connected, with the conidial stage of *Xenosporella Thaxteri*. Figs. 23 and 24 represent an ascus and ascospores. Drawings from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 26

Figs. 1–2. *Helicoon farinosum* Linder

Conidiophores and conidia. The short, almost ovoid conidia with their definite septa and the usually distinct conidiophores separate this species from *H. sessile,* which it closely resembles. Drawings from type material. × 500.

Figs. 3–5. *Helicoon auratum* (Ellis) Morgan

Conidia and conidiophores. The conidiophores, fuscous below and dilute fuscous above, usually bear the golden-yellow spores one at a time, although, as is indicated by the presence of sporogenous teeth, they are capable of producing several conidia. Fig. 5 demonstrates the hygroscopic nature of the spore by its slight uncoiling and pronounced elongation. × 500.

Figs. 6–8. *Helicoon fuscosporum* Linder

Conidiophores and conidia from type material. × 500.

Figs. 9–10. *Helicoon reticulatum* Linder

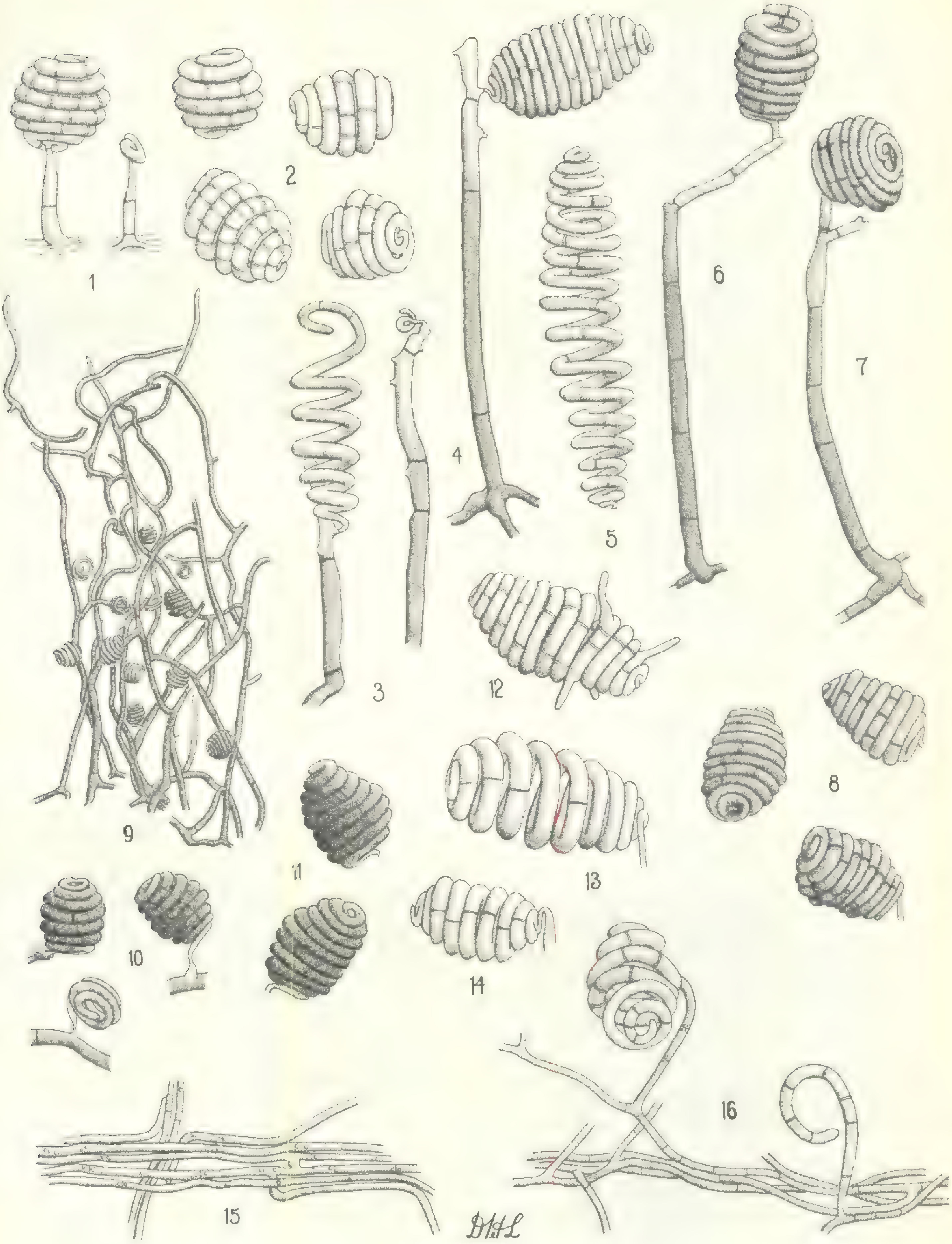
The conidiophores of this species are comparable to those of *Helicosporium lumbricoides* in that they branch and anastomose frequently, as is true also of *Helicoon ellipticum.* Drawings from type material. × 500.

Fig. 11. *Helicoon ellipticum* (Peck) Morgan

The conidiophores not shown here are the same as those of *H. reticulatum.* The conidia of this species are, however, conspicuously larger than are those of *H. reticulatum.* × 500.

Figs. 12–16. *Helicoon sessile* Morgan

In fig. 12 is shown a germinating conidium. Figs. 15 and 16 are both drawn from material in culture. Fig. 15 shows a portion of a strand of parallel hyphae which apparently serve for the transportation of food material and of retaining moisture, as is explained in Part I of the text. All drawings from material collected by the writer. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 27

Figs. 1–2. *Helicodendron triglitziensis* (Jaap) Linder

In fig. 1 is shown a conidiophore which has arisen from the repent sterile mycelium and bears two groups of conidia that produce tangled chains. Fig. 2 is an edgewise view that illustrates the seriate arrangement of the conidial coils. × 500.

Figs. 3–4. *Helicodendron hyalinum* Linder

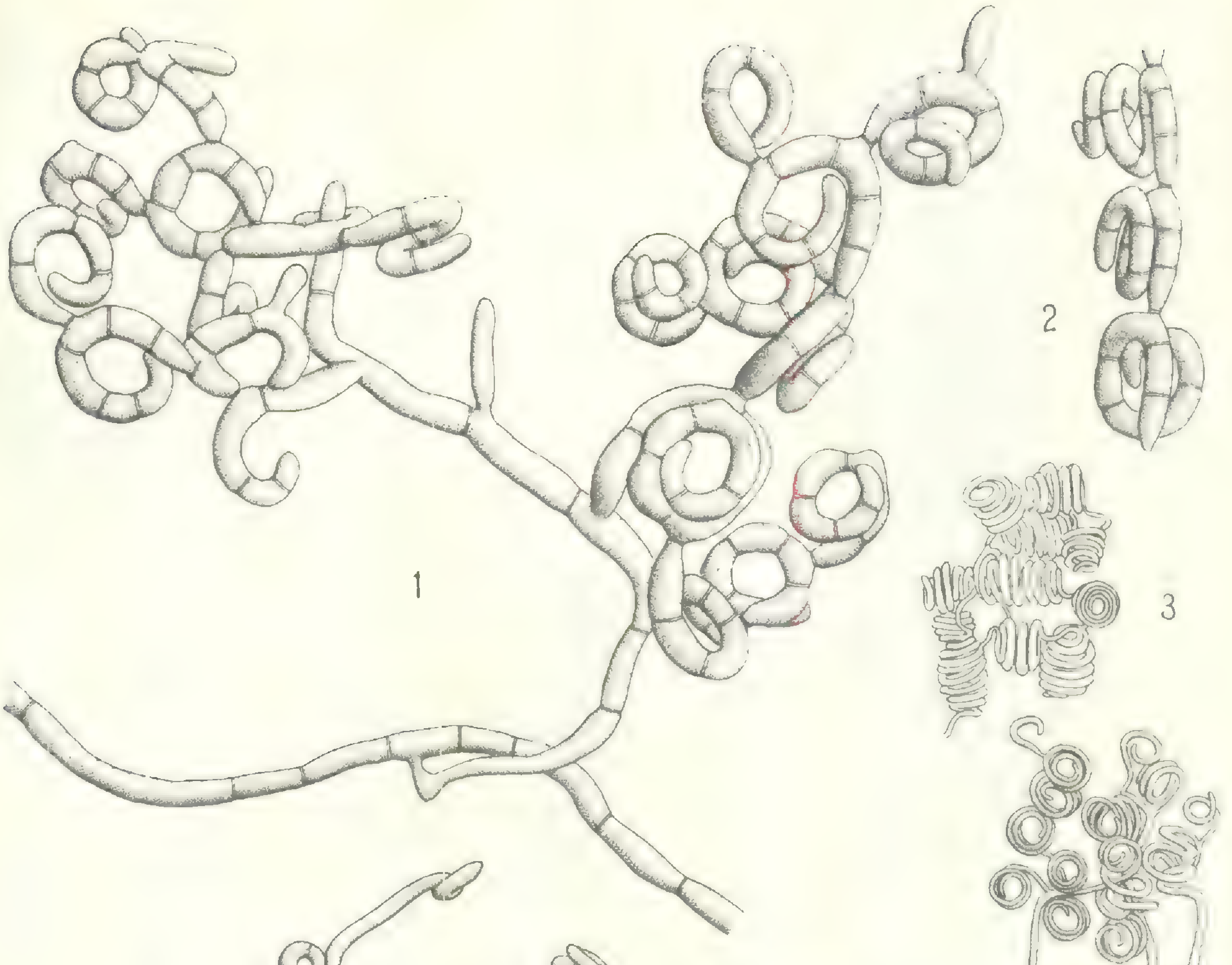
Conidia and conidiophores from type material. × 500.

Figs. 5–6. *Helicodendron fuscum* (B. & C.) Linder

Conidia and conidiophores from type material. × 500.

Figs. 7–11. *Helicodendron tubulosum* (Reiss) Linder

Conidia and conidiophores. The drawings represented by figs. 7 and 11 are both from specimens growing in culture, the remainder are from specimens growing on the natural substratum. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 28

Fig. 1. *Hobsonia mirabilis* (Peck) Linder

A section through a sporodochium showing the rather compact arrangement of the hyphae, and the conidia borne at or near the surface of the colony. Drawing from material growing on corncob in Tennessee. × 120.

Figs. 2–5. *Hobsonia mirabilis* (Peck) Linder

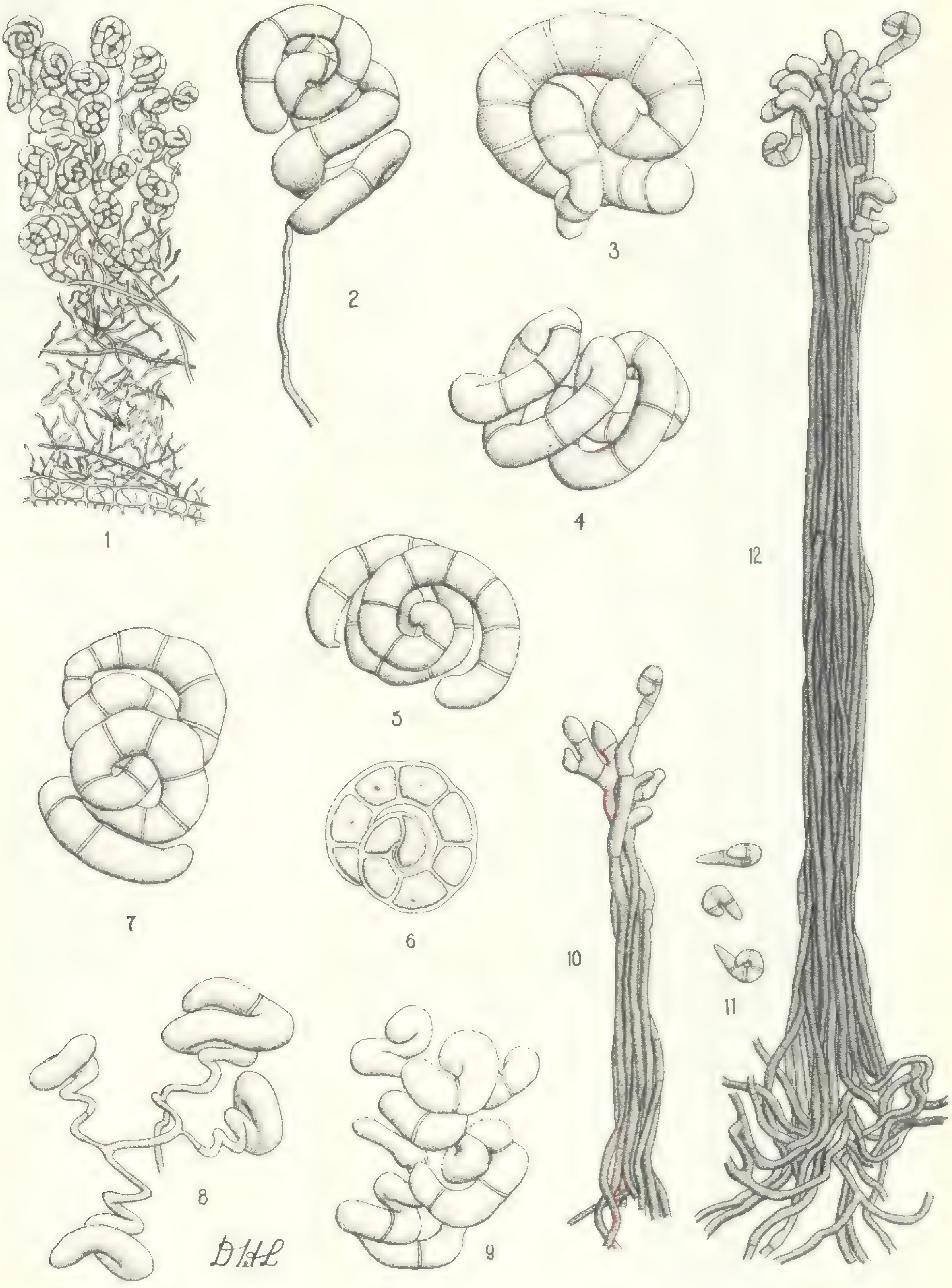
Conidia. In fig. 2 the simple and but slightly twisted conidiophore is shown, and in fig. 5, a conidium which has begun to proliferate. × 500.

Figs. 6–9. *Hobsonia gigaspora* Berkeley

Figs. 6 and 7 represent simple conidia; fig. 8 illustrates the branching and spiral twisting of the conidiophores just below the conidia; while in fig. 9 is shown a proliferating conidium. All the drawings were made from material collected in Grenada (*Thaxter*, Grand Etang, Grenada). × 500.

Figs. 10–12. *Helicostilbe simplex* Petch

The conidiophores, as shown in figs. 10 and 12, are closely aggregated to form synnemata which bear the sporogenous teeth apically. The conidia of this species strongly resemble those of *Helicoma simplex* and *Helicoma fasciculatum*. Drawings from type material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

PLATE 29

Fig. 1. *Everhartia lignitalis* Thaxter

A substipitate sporodochium. The rounded mass at the summit is composed of spores that are held together by the gelatinous matrix in which they are imbedded. Freehand drawing from type material. × 22.5 approx.

Fig. 2. *Everhartia lignitalis* Thaxter

Conidiophores from apex of sporodochial stipe. Preparation obtained by crushing the material on the object glass. × 500.

Figs. 3–4. *Everhartia lignitalis* Thaxter

The conidia in fig. 3 are shown in optical section, × 1145; those in fig. 4, × 500.

Fig. 5. *Everhartia candida* Thaxter

A pulvinate sporodochium. Freehand drawing from type material. × 22.5 approx.

Figs. 6–7. *Everhartia candida* Thaxter

The conidia in fig. 6 are shown in optical section, × 1145; those in fig. 7, × 500.

Figs. 8–9. *Everhartia hymenuloides* Saccardo & Ellis

The conidium in fig. 8 is shown in optical section, × 1145; those in fig. 9, × 500. From type material.

Figs. 10–14. *Troposporella fumosa* Karsten

Conidia and conidiophores are shown in figs. 10 and 12–14, all × 500. In fig. 11 the sporodochium with its dry granular surface is shown, × 20. All drawings are made from type material.

Figs. 15–17. *Drepanoconis larvaeformis* Spegazzini

In fig. 15, the drawings are of conidia from the type material of *Drepanoconis fructigena* (*Rick, 42*). Figs. 16 and 17 are from the type material of *D. larvaeformis* (*Balansa, 3758*). The conidiophores, as shown in fig. 16, are surrounded by a gelatinous hyaline matrix, and are much exceeded in length by the sterile hyphae. All figures × 500.

Fig. 18. *Drepanoconis anguisporus* Patouillard

Conidia from type material. × 500.

Fig. 19. *Delortia palmicola* Patouillard

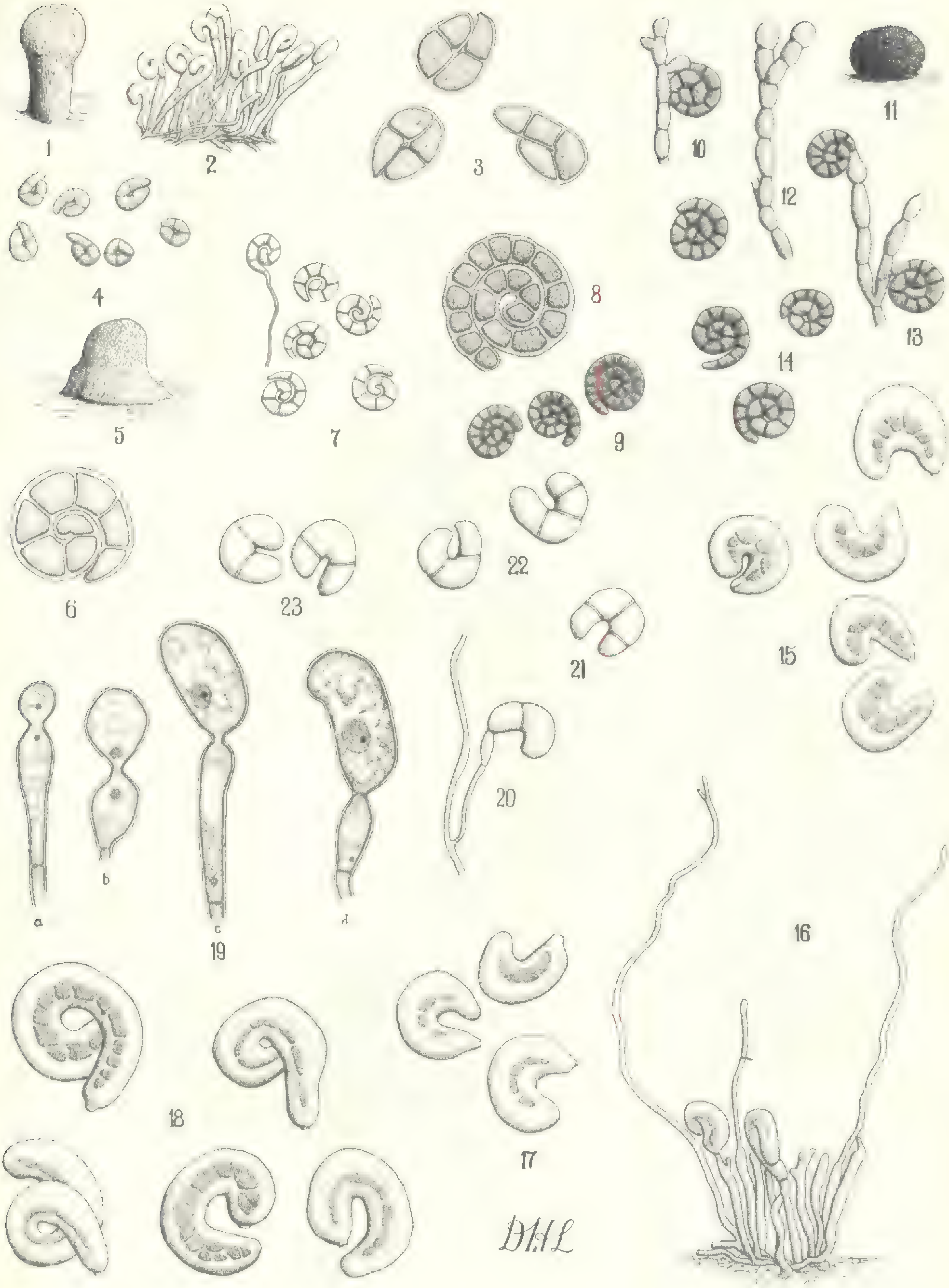
Early stages in the formation of a conidium to show the behavior of the nuclei. × 1145.

Figs. 20–21. *Delortia palmicola* Patouillard

Conidia and a conidiophore with a portion of a sterile hypha. From Liberian material. × 500.

Figs. 22–23. *Delortia palmicola* Patouillard

Conidia from British Guiana material. × 500.



LINDER—HELICOSPOREAE

Explanation of Plate

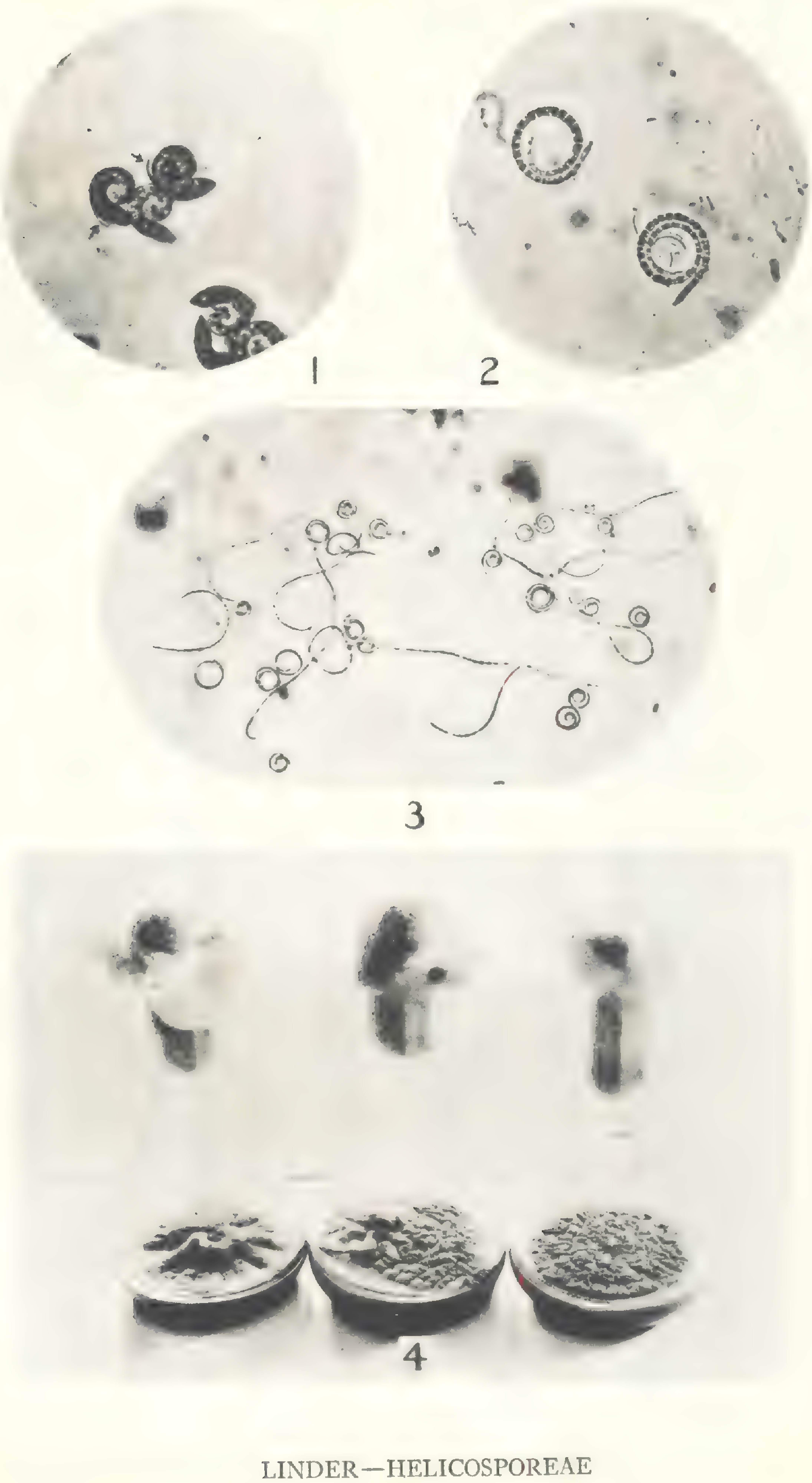
PLATE 30

Fig. 1. *Helicoma Curtisii* Berkeley
The spores are shown just previous to germination, at which time the filaments have become swollen and the exospore has been ruptured.

Fig. 2. *Helicomyces scandens* Morgan
Swollen conidia that have ruptured the exospores, fragments of which may be seen near the lower conidium.

Fig. 3. *Helicosporium aureum* (Cda.) Linder
Hygroscopic spores, some of which have uncoiled on contact with the wet agar substratum.

Fig. 4. *Helicodendron triglitziensis* (Jaap) Linder, and *H. tubulosum* (Reiss) Linder
Comparative cultures of 2 species. The flask on the right contains a colony of *H. tubulosum*, that on the left a colony of *H. triglitziensis*, and in the center the two species are contrasted.



LINDER—HELICOSPOREAE

COCKAYNE, BOSTON

Explanation of Plate

PLATE 31

Fig. 1. *Hobsonia mirabilis* (Peck) Linder

Sporodochia on a corncob. The white arrows point to a few of the sporodochia. × 1.2.

Fig. 2. *Helicoma Curtisii* Berkeley

The dark, effuse, hirsute colonies growing on decaying wood. × 1.2.

Fig. 3. *Helicomyces scandens* Morgan

The effuse and non-fasciculate younger portions of the colony are at the right, while the older part, indicated by the arrow, are characterized by denticulate appearance. It is in this older part that the hyphae have become fasciculate and the setae have developed. × 1.2.

Fig. 4. *Gyroceras plantaginis* (Cda.) Sacc.

Not included in the present paper.

Fig. 5. *Helicoon ellipticum* (Peck) Morgan.

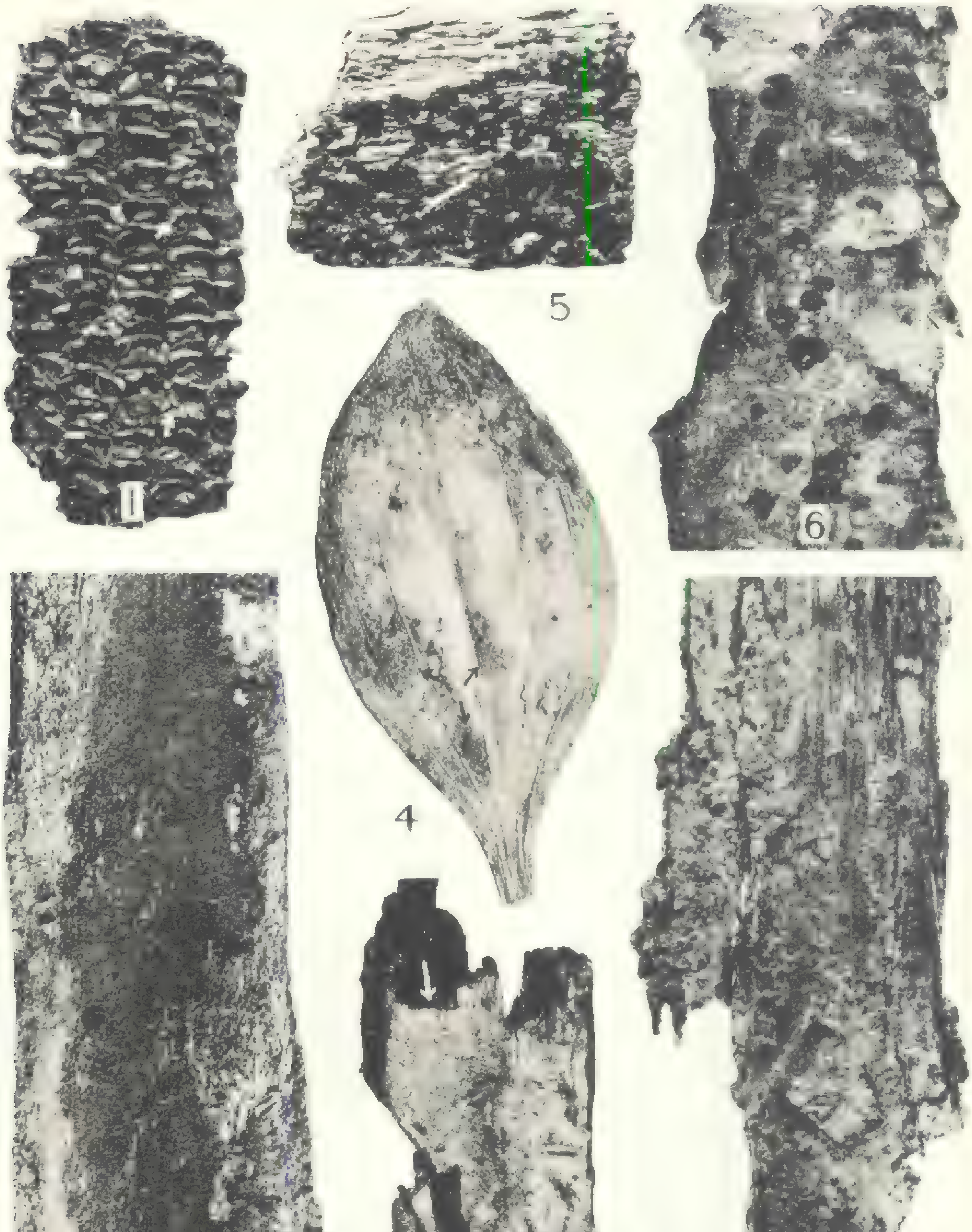
The colonies are loose, cottony, and easily separable from the substratum of decaying wood. At first they are circular but tend to coalesce to form irregular masses. × 1.2.

Fig. 6. *Helicoma proliferens* Linder

The dark, circular, minutely hirsute colonies of this species apparently grow best near the lenticels in the bark. × 1.2.

Fig. 7. *Helicosporium lumbricoides* Sacc. emend. Matruchot

The colonies form an effuse cottony layer over the substratum. The light color is due to the hyaline to subhyaline extremities of the conidiophores and the abundance of conidia. × 1.2.



LINDER—HELICOSPOREAE

COCKAYNE, BOSTON

Annals of the Missouri Botanical Garden

Vol. 16 NOVEMBER, 1929 No. 4

NEW AGAVES FROM SOUTHWESTERN UNITED STATES[1]

J. M. GREENMAN

Curator of the Herbarium of the Missouri Botanical Garden
Professor in the Henry Shaw School of Botany of Washington University

AND

EVA M. FLING ROUSH

Jessie R. Barr Fellow in the Henry Shaw School of Botany of Washington University

Two specimens of *Agave* were submitted recently to the Missouri Botanical Garden by Mr. W. I. Beecroft of Escondida, California, for identification. These plants had been collected at an altitude of 4000–5000 ft. in the mountains of southwestern Nevada. They seem to accord with material in the herbarium which Dr. Engelmann had referred doubtfully to *Agave utahensis*, as a possible variety. A more careful examination shows that they differ from that species, of which the type material is in the Garden Herbarium, in several important details.

In the comprehensive studies of the Agaves of the United States by Miss A. Isabel Mulford under the careful direction of Dr. Wm. Trelease, the material studied by Dr. Engelmann was merged, possibly because of its fragmentary nature, with *Agave utahensis*. A critical comparison of these fragments and the specimens from southwestern Nevada with the type of *A. utahensis* shows the following striking differences:

[1] Issued December 30, 1929.

A. utahensis	*A. utahensis* var. *nevadensis*
Leaves strongly inrolled in the terminal portion	Leaves not strongly inrolled in the terminal portion
Terminal spine stoutish, deeply grooved, 2.5 cm. or less long	Terminal spine slender, flat or shallowly grooved on the upper surface, 5 cm. or more long
Perianth-tube very slender, 4–5 mm. long	Perianth-tube stoutish, 1–2 mm. long
Perianth-segments 10–12 mm. long	Perianth-segments 8–10 mm. long

These differences warrant the recognition of this plant at least as a distinct variety which is characterized as follows:

Agave utahensis Engelm. in Watson, Bot. King. Exp. 497. 1871.

Var. **nevadensis** Engelm.[1] in herb. Plate 32.

Stem short, thick, 3–4.5 cm. in diameter; leaves lance-attenuate, 1–2.5 dm. long, 2 cm. or less broad, dilated at base (3–5 cm.), glaucous and minutely scurfy on both surfaces; terminal spine slender, linear-attenuate, grayish, pungent, 3–6 cm. long; marginal prickles 2–4 cm. apart, flattened, grayish white, friable, mostly recurved, surrounded at the base, as in the case of the terminal spine, by a narrow dark brownish area; leaf-margins herbaceous, sinuate, becoming minutely serrulate on the upper portion of the dilated base; flowers about 2.5 cm. long, ovary 10 mm. or less long, perianth-tube stoutish, 1–2 mm. long, perianth-segments 8–10 mm. long.—California: Ivanpah, Mohave Desert, May, 1882, *S. B. & W. F. Parish 414* (Mo. Bot. Gard. Herb.), TYPE. Specimens from southwestern Nevada sent recently to the Missouri Botanical Garden by Mr. W. I. Beecroft for identification appear to belong to this variety.

Specimens in the Missouri Botanical Garden Herbarium from St. George, Utah, collected by Dr. Edward Palmer in 1877, were

[1] **Agave utahensis** Engelm. var. **nevadensis** Engelm. in herb. Perennis; caulibus brevibus, crassibus, 3–4.5 cm. diametro; foliis lanceo-attenuatis, 1–2.5 dm. longis, 2 cm. vel minus latis ad basin (3–5 cm.) dilatatis, utrinque glaucis et minutissime porriginosis; spina terminali tenui, lineari-attenuata, cinerea, 3–6 cm. longa; aculeis complanatis, cinero-albidis, friabilis, plerumque recurvatis, circa basin ferrugineis, 2–4 cm. remotis; marginibus foliorum ad basin dilatatis, integris vel serrulatis; floribus ca. 2.5 cm. longibus; ovario 10 mm. vel minus longo; tubo perianthii 1–2 mm. longo; lobis perianthii 8–10 mm. longis.—California: Ivanpah, Mohave Desert, May, 1882, *S. B. & W. F. Parish 414* (Mo. Bot. Gard. Herb.), TYPE.

mentioned by Miss A. Isabel Mulford[1] as a thick-leaved form of *Agave utahensis* Engelm. and were designated by Dr. William Trelease as "*A. utahensis* var. *nevadensis*." However, the plant which Dr. Engelmann characterized and recorded in his unpublished notes as *Agave utahensis* var. *nevadensis* was collected by S. B. and W. F. Parish at Ivanpah, Mohave Desert, in May, 1882. A further study of the Palmer plant in the light of additional material shows that it is not only specifically distinct from *A. utahensis* and its variety *nevadensis*, but apparently represents an undescribed species belonging to the section *Geminiflorae*. The following description records the outstanding characters of the species:

Agave scaphoidea[2] Greenman & Roush, n. sp. Leaves linear-lanceolate, thick and rigid, openly concave, 12–35 cm. long, 1.5–3.5 cm. broad, slightly narrowed toward the base, minutely roughened on the surface, gradually attenuate above the middle; terminal spine stout, reddish-brown, pungent, 4 cm. long, openly grooved for about one-half its length and decurrent along the leaf-margin for nearly or quite 4 cm.; marginal prickles short-triangular, slightly curved, reddish-brown, papillate, about 3 cm. apart on the otherwise straight and herbaceous leaf-margins; inflorescence spicate; flowers in pairs, 3–3.5 cm. long; ovary 10–12 mm. long; tube of the perianth 6-8 mm. long, slender; perianth-segments oblong, 15–17 mm. long, obtusish; mature fruit not seen.—Utah: St. George, May, 1877, *Ed. Palmer* (Mo. Bot. Gard. Herb. Nos. 124604 TYPE, 124605, 124606, 124607 in part).

This species has been confused hitherto with *A. utahensis* of

[1] Mulford, A. Isabel. Agaves of the United States. Rept. Mo. Bot. Gard. **7**: 78. 1896.

[2] **Agave scaphoidea** Greenman & Roush, n. sp. Folia lineari-lanceolata, crassa et rigida, aperte concava, 12–35 cm. longa, 1.5–3.5 cm. lata, versus basin paulo angustata, utrinque minutissime aspera, supra mediam gradatim attenuata; spina terminali rigida, ferruginea, 4 cm. longa, plus minusve canaliculata, ad marginem folii decurrenti; aculeis brevi-triangularis, paululo curvatis, ferrugineis, papillosis, circiter 3 cm. remotis; inflorescentia spicata; floribus binis, 3–3.5 cm. longis; ovario 10–12 mm. longo; tubo perianthii 6–8 mm. longo, tenui; lobis perianthii oblongis, 15–17 mm. longis, obtusis; capsula ignota.—Utah: St. George, coll. of May, 1877, *Ed. Palmer* (Mo. Bot. Gard. Herb. Nos. 124604 TYPE, 124605, 124606, 124607 in part).

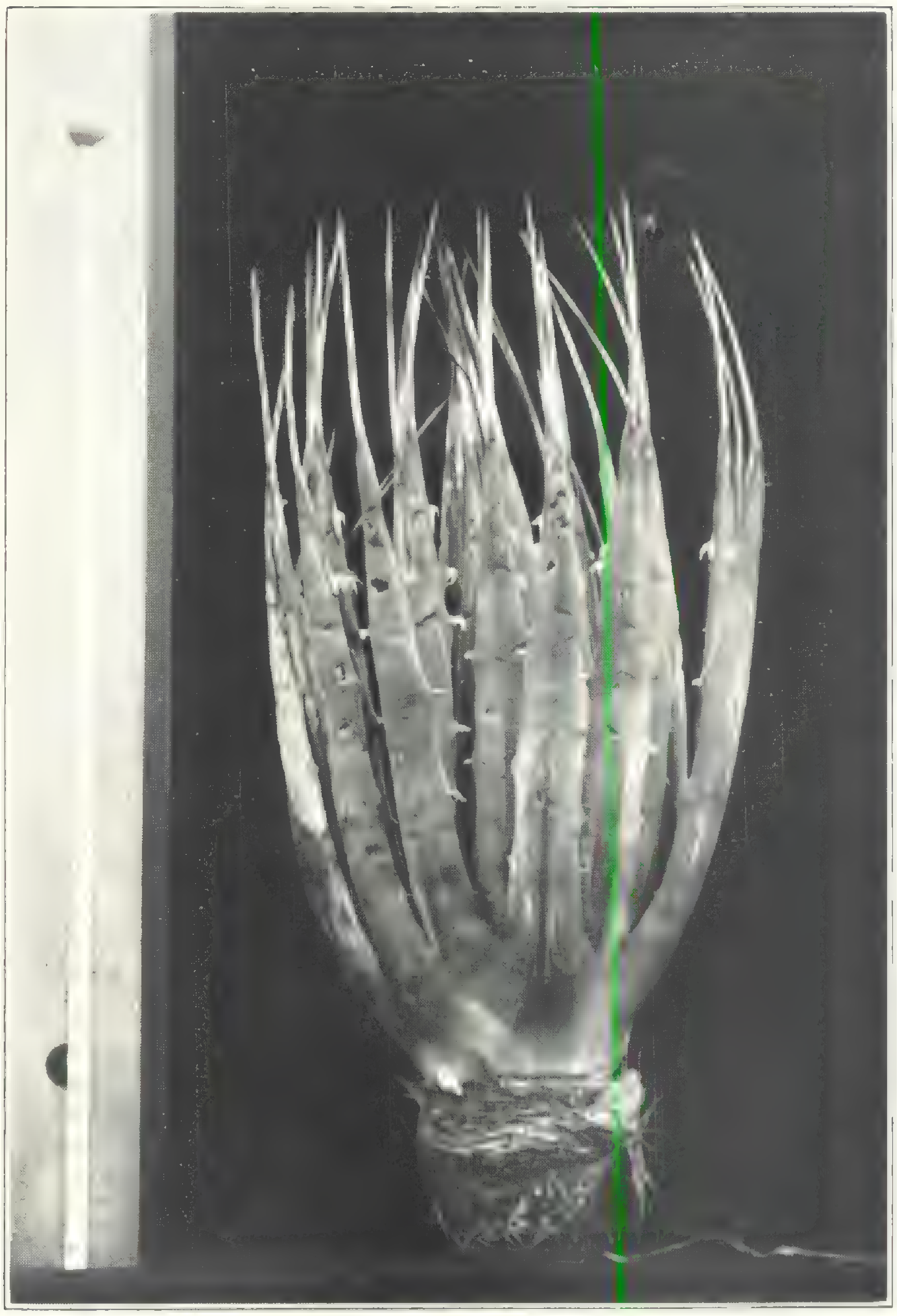
Engelm. from which, however, it is clearly distinct as shown by the following tabulated characters:

Agave utahensis	*Agave scaphoidea*
Leaf-margins sinuate	Leaf-margins straight
Prickles approximate, gray, friable	Prickles remote, reddish, papillate, rigid
Terminal spine slender, 2 cm. long, grayish, involute for practically its entire length	Terminal spine stout, 4 cm. long, reddish-brown, openly grooved for about one-half its length
Perianth-segments 10–12 mm. long, tube of the perianth 4–5 mm. long	Perianth-segments 15–17 mm. long, tube of the perianth 6–8 mm. long

Explanation of Plate

PLATE 32

Agave utahensis Engelm. var. *nevadensis* Engelm. in herb.
Nevada.
From a living plant collected by Mr. G. E. Barrett
in southwestern Nevada.



GREENMAN AND ROUSH—NEW AGAVES

STUDIES IN THE UMBELLIFERAE. II

MILDRED E. MATHIAS

Research Assistant, Missouri Botanical Garden
Formerly Jessie R. Barr Fellow in the Henry Shaw School of Botany of Washington University

1. Neoparrya, a New Genus of the Umbelliferae

Neoparrya[1] n. gen. of the Umbelliferae. Herbaceous, acaulescent perennial. Leaves pinnatisect. Inflorescence spreading; peduncles exceeding the leaves; involucre absent; involucel of small, inconspicuous bracts. Calyx teeth persistent. Stylopodium lacking. Fruit oblong, glabrous; ribs slightly developed; oil tubes small, numerous, scattered in the pericarp; strengthening cells absent.

The type species is **Neoparrya lithophila,**[2] n. sp. Plate 33.

Seseli Nuttallii Gray, Proc. Am. Acad. **8**: 287. 1870, as to Parry collection, No. 83.

Plant acaulescent, about 1.5 dm. high; leaves petiolate, oblong-lanceolate in outline, 8–10 cm. long, about 2.5 cm. broad, somewhat rigid, glabrous, ultimate segments linear, 5–20 mm. long; umbels several-rayed, rays 0.5–1.5 cm. long; involucel bracts linear-lanceolate, about 3 mm. long; styles 2–3 mm. long, persistent; fruit 3–5 mm. long, lateral and dorsal ribs inconspicuous.

Type specimen: *Dr. C. C. Parry 83*, "on rocks, Huefano Mountains, New Mexico," Sept. 1867 (TYPE in the Gray Herbarium of Harvard University; isotypes in the Missouri Botanical Garden Herbarium).

[1] **Neoparrya** Mathias, n. gen.—Herba perennis, acaula. Folia pinnatisecta. Radii umbellae expandi; pedunculi foliis longiores; involucra nulla; involucella parvae obscurae bracteae. Calycis dentes persistentes. Stylopodium nullum. Fructus oblongus, glaber; jugae obscurae; vittae parvae, multae, in pericarpio hinc inde distributae; cellae firmantes nullae.

[2] **Neoparrya lithophila** Mathias, n. sp.—Planta acaula, circa 1.5 dm. alta; foliis petiolatis, in circumscripto oblongo-lanceolatis, 8–10 cm. longis, circa 2.5 cm. latis, subrigidis, glabris, ultimis segmentis linearibus, 5–20 mm. longis; umbellis multiradiatis, radiis 0.5–1.5 cm. longis; involucellae bracteis lineari-lanceolatis, circa 3 mm. longis; stylo 2–3 mm. longo, persistente; fructibus 3–5 mm. longis, lateralibus dorsalibusque jugis obscuris.—Collected "on rocks, Huefano Mountains, New Mexico," Sept. 1867, *Dr. C. C. Parry 83* (Gray Herb., TYPE; Mo. Bot. Gard. Herb., isotypes).

Issued December 30, 1929.

This species is the *Seseli Nuttallii* Gray, Proc. Am. Acad. **8**: 287. 1870, in part. Gray says in describing the species that it "has been for several years known to me in a specimen collected by Nuttall, in flower only, and presented by the kind Mr. Durand. It is ticketed by Nuttall '*Cynomarathrum saxatile*,' but it is not published. The same plant, in fruit only, was gathered by Dr. Parry in 1867, in the mountains of the northeastern part of New Mexico." The Nuttall specimen above mentioned, which is now in the Gray Herbarium, was examined in connection with this study as was also the Parry collection; the two plants are not congeneric. Watson, in the Proceedings of the American Academy **22**: 475. 1887, made the same conclusion: "The plant of Parry's collection which was included with Nuttall's under *Seseli Nuttallii* remains uncertain. It is scarcely a congener of the *Seseli Hallii*, Gray, described with it. In the very ripe fruit of Parry's specimen the albumen is apparently surrounded by a thin continuous layer of resinous matter, while what appear to be empty vittae are scattered through the somewhat corky pericarp." After a critical examination of specimens of the Parry collection of 1867, No. 83, from the Gray Herbarium and the Missouri Botanical Garden Herbarium, they were found to merit generic recognition.

The genus is known only from the type locality in northern New Mexico. It was collected by Dr. Parry, in whose honor it is named, at Huerfano Peak near Servilleta, Taos County. Dr. Parry was the botanist on the Pacific Railway Expedition made from Salina, Kansas, to the Pacific. The party crossed the Sangre de Cristo Mountains in southern Colorado and descended the Rio Grande to Albuquerque, New Mexico, and it was on this expedition that Parry visited the region he designated as "Huefano Mountains."

The outstanding characteristic of the genus is the position of the oil tubes which are scattered throughout the pericarp as illustrated in the accompanying microphotograph (pl. 33) of a microtome section of the fruit. The simply pinnate leaves and conspicuous reflexed umbel rays are outstanding characters more easily noted.

2. Eryngium Wolffii, New Name

Eryngium Wolffii, new name

E. mexicanum Wats. acc. to Wolff, Pflanzenreich **61:** 178. *fig. 30.* 1913, non *E. mexicanum* Wats. Proc. Am. Acad. **26:** 136. 1891.

Herbaceous perennial, about 3 cm. high; roots many-fibrous; stems several, slender, suberect, trifurcately branched above; leaves numerous, sheathing at the base, lanceolate to oblong-ovate in general outline, 1–1.5 cm. long, deeply and irregularly pinnatisect, lobes linear-lanceolate, entire or irregularly dentate; inflorescence terminal on slender peduncles 1–10 cm. long, heads oblong-ovate, 1–1.5 cm. long, terminated by a linear, foliaceous appendage, entire or cleft at the apex; about 10 linear-lanceolate, entire, rigid, involucral bracts; fruit ovoid, about 2 mm. long, subterete in cross-section, papillose-echinate.

Type specimen: *Pringle 3180*, shallow ponds, Flor de Maria, State of Mexico, 1 Aug. 1890 (TYPE in the Gray Herbarium of Harvard University; cotypes in the Missouri Botanical Garden Herbarium, the Herbarium of the Academy of Natural Sciences, Philadelphia, the University of Chicago Herbarium, the Herbarium of the Field Museum of Natural History, the Herbarium of Carnegie Institute, Pittsburgh).

Distribution: Mexico in the states of Mexico and Morelos.

Specimens examined: shallow ponds, Flor de Maria, Mexico, 1 Aug. 1890, *Pringle 3180* (Gray Herb. TYPE, Mo. Bot. Gard. Herb., Phila. Acad. Herb., Univ. Chicago Herb., Field Museum Herb., Herb. Carnegie Inst.); Cerro de los Valgos, Morelia, alt. 2300 m., 1907, *Arsène* (U. S. Nat. Herb. 1157098).

Eryngium mexicanum as described by Watson[1] was based on a collection made by C. G. Pringle at Del Rio, State of Mexico, August 30, 1890, namely, No. 3229. Upon critical examination of cotype material of this number, it has been identified as *E. phyteumae* (*phyteumatos*) Delar.[2] The species, *E. mexicanum*, as described by Watson,[1] therefore goes to synonymy under *E. phyteumae* Delar. This is the position given the species by

[1] Watson, Proc. Am. Acad. **26:** 136. 1891.

[2] Delar. Eryng. Hist. 51. *pl. 21.* 1808.

Wolff[1] in his treatment of the genus *Eryngium* for the 'Pflanzenreich.' However, Wolff[2] retains the specific name, *E. mexicanum* Wats., for the plant collected by Pringle at Flor de Maria, State of Mexico, August 1, 1890, namely No. 3180. The latter plant has been found to be specifically distinct from *E. mexicanum*, as originally described, and, since that name has fallen to synonymy, must be given a new name. The name *Wolffii* is proposed for the species in honor of Hermann Wolff.

3. A Pimpinella New to North America

The common pimpernel, *Pimpinella Saxifraga* L., a native of Europe, has been introduced into waste places in eastern North America, becoming well established in certain localities. This form of the species has in all cases been recorded as glabrous, but a few specimens show a slight tendency toward a hirsute-pubescent condition.

During the past summer Dr. Harold St. John sent the author for determination a plant collected by Professor Morton E. Peck in a "meadow, 3½ miles s. e. of Roche Harbor, San Juan Islands, Washington, July 24, 1923," namely, *No. 13099.* Upon critical examination this plant proved to be *Pimpinella Saxifraga* L. subspecies *nigra* (Mill.) Gaud., as defined in the most recent survey of the genus by Wolff[3] for the 'Pflanzenreich.'

This subspecies is clearly distinguished by its conspicuous hirsute pubescence from the common "glabrous" *P. Saxifraga* previously reported in North America. The plant is of special interest not only as a new introduction into this country, but as the first record of the genus *Pimpinella* becoming established on the west coast or in western North America.

[1] Wolff, Pflanzenreich **61**: 188. 1913.
[2] Wolff, *Ibid* **61**: 178. 1913.
[3] Wolff, Pflanzenreich **90**: 302. 1927.

Explanation of Plate

PLATE 33

Neoparrya lithophila Mathias, from the type specimen, *Parry 83*, in the Gray Herbarium of Harvard University.

Superimposed on the type sheet is a microphotograph of a cross-section in the median plane of a mature fruit, taken from an isotype in the Missouri Botanical Garden Herbarium. × 25.

MATHIAS—STUDIES IN THE UMBELLIFERAE. II

NOTES ON SOUTHWESTERN PLANTS

MILDRED E. MATHIAS

Research Assistant, Missouri Botanical Garden
Formerly Jessie R. Barr Fellow in the Henry Shaw School of Botany of Washington University

1. Gaura suffulta Engelmann

In a collection of plants made in Oklahoma by Robert Stratton was a specimen of *Gaura* which could not be placed in any species known to occur in that state. After a critical survey of the genus and a comparison with type material it was found to be conspecific with *G. suffulta* Engelm.[1] This species has been known previously only from southern Texas, and its distribution as given by Small[2] is "On prairies or mountain slopes, Texas and northern Mexico," and by Coulter[3] "From the Colorado to the Lower Rio Grande, west to the Pecos and New Mexico." The accompanying map (fig. 1) shows the range of distribution of the species as represented in the Herbarium of the Missouri Botanical Garden, and gives the northern extension of the range as indicated by the Stratton specimen from the Arbuckle Mountains of southern Oklahoma, the Emig collections from the same region, and the Palmer and Glatfelter collections from Fort Worth and Dallas.

This species as described by Engelmann is quite distinct in its characters but has been poorly defined in subsequent works. Consequently a great amount of southwestern material of the genus *Gaura* has been erroneously referred to *G. suffulta*. The work of Wooton and Standley[4] in 1913 in segregating several new species from this complex has partially reinstated the species to the status originally given it by Engelmann. Its outstanding characteristics are a sessile, glabrous, oblong fruit somewhat constricted toward the apex, glabrous buds and caducous bracts prominently ciliate on the margins. The following material in

[1] Engelm. in Gray, Bost. Jour. Nat. Hist. 6 [Pl. Lindh. 2]: 190. 1850.
[2] Small, Fl. Southeastern U. S. ed. 2. 848. 1913.
[3] Coulter, Contr. U. S. Nat. Herb. 2 [Bot. West. Texas]: 118. 1891.
[4] Wooton and Standley, Contr. U. S. Nat. Herb. 16: 152–154. 1913.

Issued December 30, 1929.

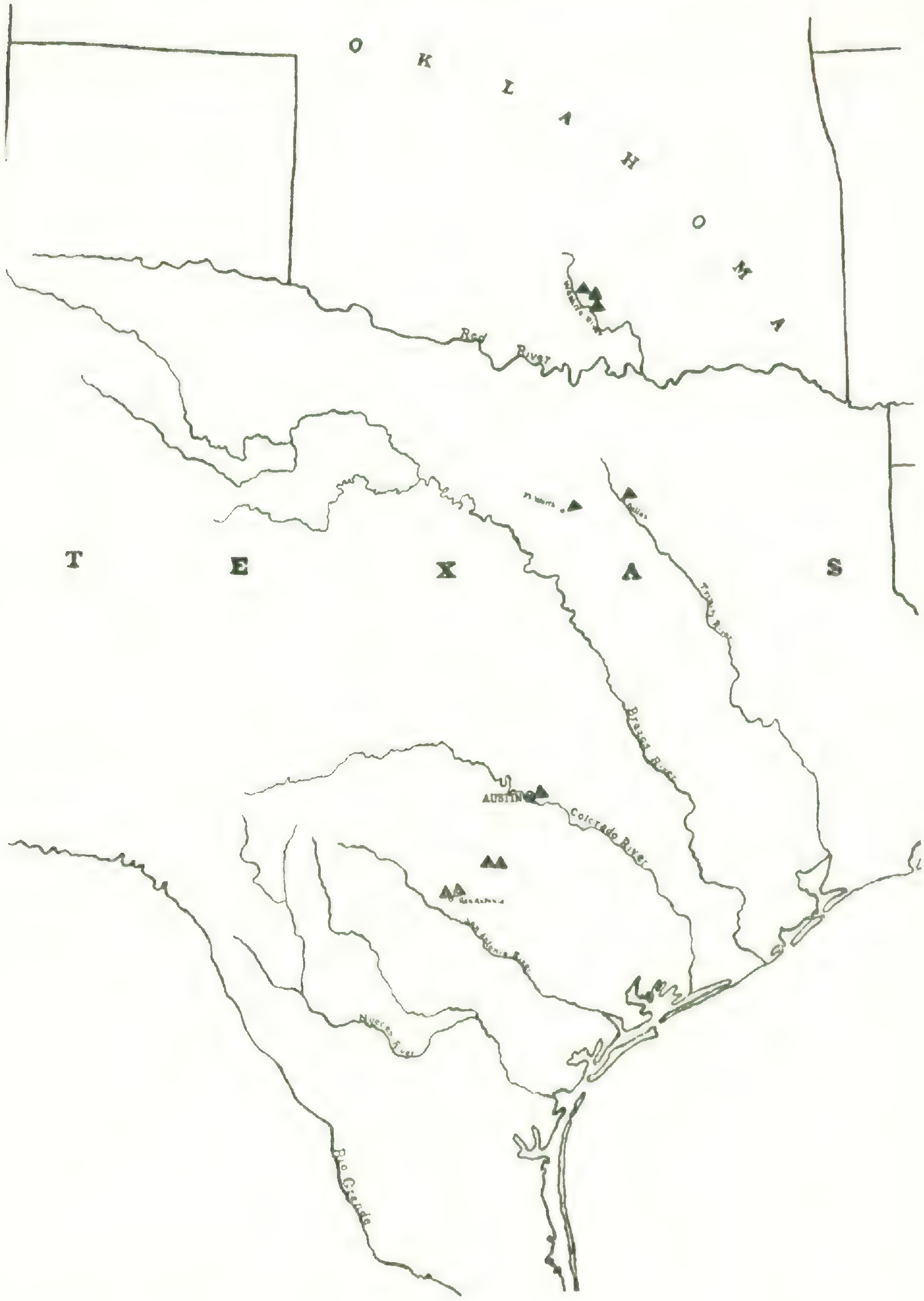


Fig. 1. Distribution of *Gaura suffulta*.

the collections of the Missouri Botanical Garden Herbarium has been found referable to the species as defined by Engelmann:

OKLAHOMA: rocky soil on mountain top, Price's Falls, Murray Co., 30 April, 1926, *Stratton 28;* Arbuckle Mts., Crusher, 12 May, 1916, *Emig 574;* Arbuckle Mts., near Davis, 21 June, 1917, *Emig 829.*

TEXAS: New Braunfels, May–June, 1847–8, *Lindheimer 611* (TYPE); New Braunfels, April, 1851, *Lindheimer 805;* dry hills, Austin, 9 May, 1872, *Hall 212;* rocky limestone hillsides, Ft. Worth, Tarrant Co., 24 May, 1918, *Palmer 3670;* San Antonio, *Wilkinson 73, 74;* tropical life zone, San Antonio, Bexar Co., 19 April, 1911, *Clemens & Clemens 697;* Dallas, 16 June, 1898, *Glatfelter.*

II. HOUSTONIA CROFTIAE BRITTON & RUSBY

Houstonia Croftiae Britton & Rusby, Trans. N. Y. Acad. Sci. **7**: 10. 1887; Coulter, Contr. U. S. Nat. Herb. **2**: 159. 1892; Greenman, Proc. Am. Acad. **32**: 284. 1897; Small, Fl. Southeastern U. S. 1108. 1903, and ed. 2. 1913.

Copious material of this species was found growing in the sand in the vicinity of Laredo, Texas, by J. Reverchon, March 21, 1903. The specimens had been referred doubtfully to *Houstonia humifusa* Gray. Upon critical examination the material was found not to represent *Houstonia humifusa* as defined by Gray and was determined from characters as *H. Croftiae.* As no authentic material of this species was available for comparison the specimen was sent to Dr. N. L. Britton, who verified the identification as *H. Croftiae* and stated that "It appears to agree exactly with my type specimen except in being a better developed and larger individual." This is a new station for this apparently rare species and seems to indicate a range for the species through southeastern Texas. The variation in size from the type material is so great that it seems worthy to mention such variations as occur by giving the following amplified description.

Houstonia Croftiae Britton & Rusby Plate 34, figs. 1–2.

A depressed-spreading annual; stems 1.5–10 cm. long, hirtellous with many scattered hairs; leaves 2–20 mm. long, oblanceolate, revolute, obtuse; stipules scarious, laciniate-dentate; flowers minute,

about 2 mm. long, sessile in the axils; calyx hirsute-pubescent; sepals linear-lanceolate; capsule subdidymous, 3 mm. high, about one-fourth inferior, hirsute-pubescent; seeds open-crateriform with a short hilar ridge.—Laredo, Texas, 21 March, 1903, *J. Reverchon 3951* (Mo. Bot. Gard. Herb.); San Diego, Duval Co., Texas, 1885, *Mary B. Croft 85* (N. Y. Bot. Gard. Herb., TYPE).

The type of the species shows these variations in stem and leaf length: the stems are from 0.4 to 2.5 cm. long and the leaves from 3 to 10 mm. in length as contrasted with the Reverchon material which has stems from 1.5 to 10 cm. long and leaves 2 to 20 mm. long; the flower and capsule sizes are approximately the same in both specimens.

This species is closely related to *H. humifusa* Gray and to *H. parviflora* Holzinger. Some of the most striking differences are shown in capsule and seed characters. *Houstonia parviflora* has a comparatively large capsule (pl. 34, fig. 3) about as broad as long, approximately three-fourths inferior and entirely glabrous. The calyx lobes are glabrous, short, and somewhat subulate. The seed is oblong-crateriform without a hilar ridge. *Houstonia Croftiae* has a smaller capsule (pl. 34, fig. 2), broader than long, less than one-fourth inferior and hirsute-pubescent. The calyx lobes are short and very hirsute. The seed is round, open-crateriform with a short hilar ridge. *Houstonia humifusa* has a comparatively small fruit (pl. 34, fig. 4), about one-fourth inferior and slightly roughened. The calyx lobes are linear-lanceolate, conspicuous, and usually recurved in the mature condition. The seed is oblong, somewhat concave on one surface with a hilar ridge extending throughout.

Explanation of Plate

PLATE 34

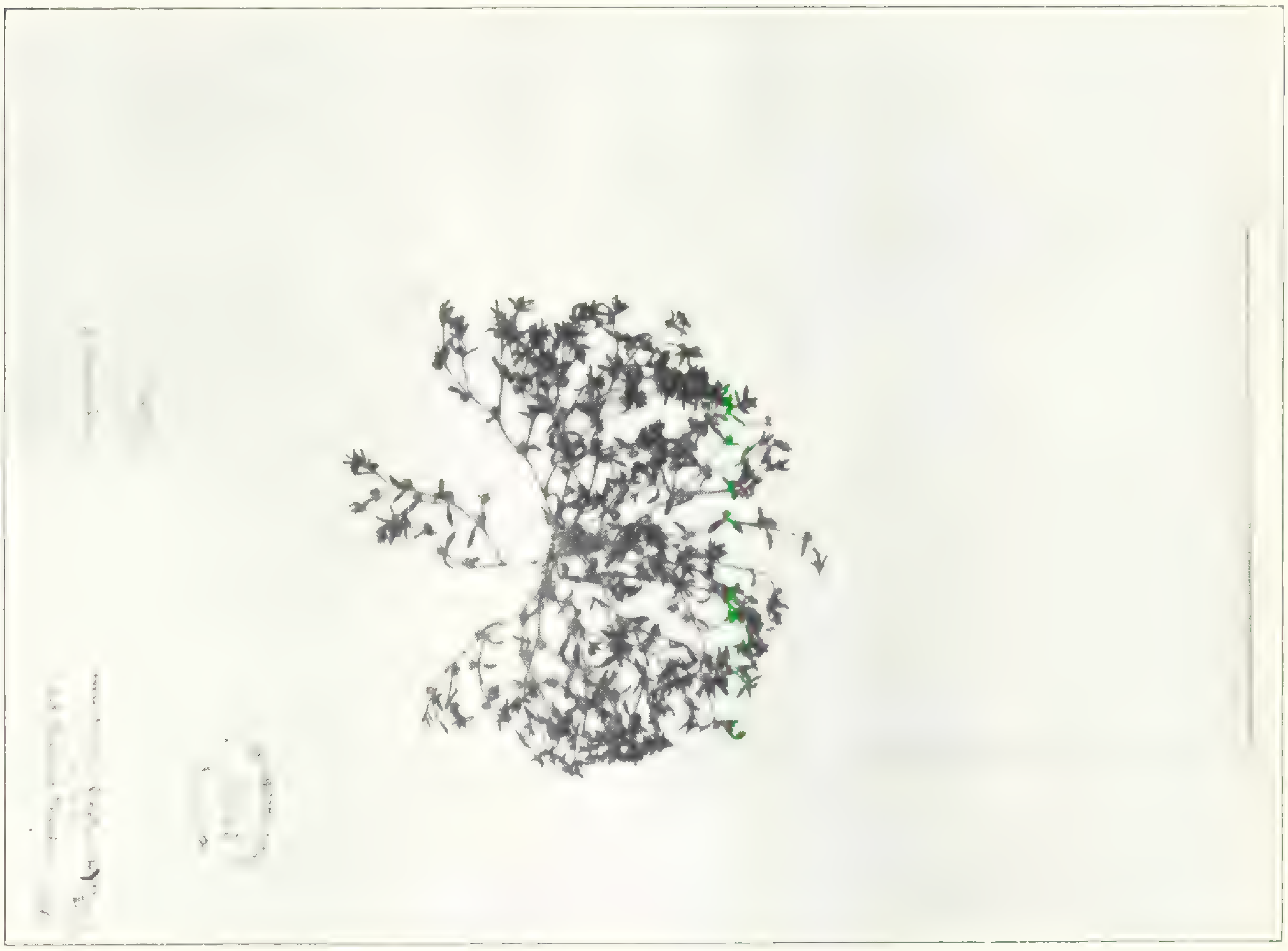
Fig. 1. *Houstonia Croftiae* Britton & Rusby, from a specimen collected by *Reverchon 3951*, in the Missouri Botanical Garden Herbarium.

Fig. 2. Mature fruit of *Houstonia Croftiae* Britton & Rusby, collected at Laredo, Texas, *Reverchon 3951*, 21 March 1903 (Mo. Bot. Gard. Herb.). × 7.

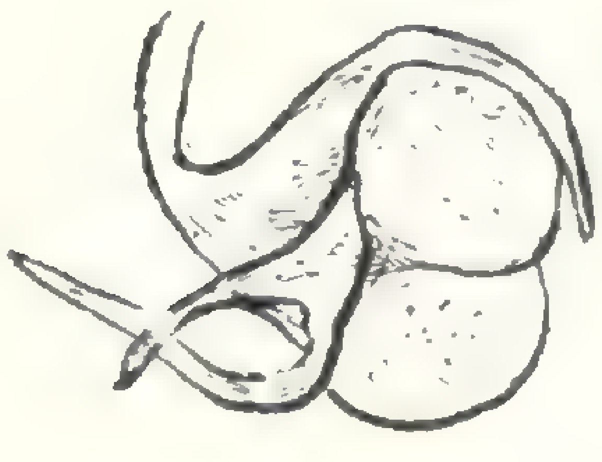
Fig. 3. Mature fruit of *Houstonia parviflora* Holzinger, collected at Vernon, Texas, *Reverchon*, 10 July 1903 (Mo. Bot. Gard. Herb.). × 7.

Fig. 4. Mature fruit of *Houstonia humifusa* Gray, collected at Raleigh, Texas, *Reverchon*, 15 April 1903 (Mo. Bot. Gard. Herb.). × 7.

1



4



3

2

MATHIAS—SOUTHWESTERN PLANTS

A NEW VARIETY OF SENECIO AUREUS L.[1]

J. M. GREENMAN

Curator of the Herbarium of the Missouri Botanical Garden
Professor in the Henry Shaw School of Botany of Washington University

About two years ago Mr. W. W. Ashe submitted to the writer for determination specimens of a plant which he had found in the mountainous region of western Virginia and eastern Tennessee. The plant in question is similar in habit and in all essential morphological characters to *Senecio aureus* L., a relatively common and well-known species of northeastern United States and adjacent Canada, but differs in having the lower surface of the leaves, especially those of the offshoots, densely white-tomentose in the early stages and only slightly glabrate in age. Furthermore, the leaves in the specimens from Mr. Ashe are somewhat thicker and firmer in texture and tend more strongly to an oblong-ovate outline than in typical *Senecio aureus* L. So far as known, this new variety has been found only in the valleys of the Middle and South Forks of the Holston River in western Virginia and eastern Tennessee, where it has been observed and collected by Mr. Ashe at a half dozen or more stations.

The origin of the plant is not known. It may be a mutant or, on the other hand, it may be a hybrid. There are some indications that it may be a hybrid between *Senecio aureus* L. and *Senecio tomentosus* Michx. The former of these two species occurs in the valley of the South Fork of the Holston River, and the latter species is relatively common in eastern Virginia. While the habit of the new plant is like *Senecio aureus*, yet the prevailing outline of the leaves of the offshoots and those of the lower parts of the upright stem, as well as their texture and tomentose character, suggests *Senecio tomentosus*.

The plant under consideration can scarcely be regarded as worthy of specific rank; and for the present, pending experimental evidence, it is deemed advisable to designate it as a new variety. Attention was called to this interesting case of variation at the meeting of the Botanical Society of America in Nashville in 1927, with the hope that additional material might be secured and its

[1] Issued December 30, 1929.

geographical range established, but no further information has been obtained. The writer takes pleasure in naming this rather remarkable variety for Mr. W. W. Ashe, who has made many important contributions to the knowledge of our flora. A description and record of distribution may be given, as follows:

Senecio aureus L. var. **Ashei** Greenman, n. var. Plate 35.

Caulis erectus 5-12 dm. altus; foliis inferioribus longe petiolatis, oblongo-ovatis, 3–10 cm. longis, 2–7 cm. latis, crenato-serratis juventate utrinque albo-floccoso-tomentosis supra denique plus minusve glabratis.—Virginia: moist meadows, near Marion, Smyth County, May 26, 1927, *Ashe*, TYPE; near Atkins, Smyth County, May 27, 1926, *Ashe;* moist meadows, limestone valley soil, near Lodi, Washington County, May 26, 1926, *Ashe.* Tennessee: moist meadows, near Johnson City, Washington County, May 24, 1926, *Ashe.*

The type specimen is in the private herbarium of Mr. W. W. Ashe, Washington, D. C. A portion of the type and photographs are in the Missouri Botanical Garden Herbarium.

Explanation of Plate

PLATE 35

Senecio aureus L. var. *Ashei* Greenman, n. var.

From the type specimen in the herbarium of Mr. W. W. Ashe.

GREENMAN—SENECIO

STUDIES IN THE APOCYNACEAE. IIIA

A New Species of Amsonia from the South-Central States

ROBERT E. WOODSON, JR.

Research Assistant, Missouri Botanical Garden

Formerly Rufus J. Lackland Research Fellow in the Henry Shaw School of Botany of Washington University

While engaged in the preparation of a recently published monograph of the genus *Amsonia*,[1] the writer was conscious of an element not quite typical in the exsiccatae which he referred to *A. Tabernaemontana* L. var. *Gattingeri* Woodson. The anomalous specimens were characterized superficially by a pubescent calyx and more elongate, shining foliage than the typical material. The plants appeared indigenous only to Missouri, southeastern Kansas, eastern Oklahoma, and northeastern Texas. Unable to perceive unquestionable evidence of individuality, however, the specimens were referred to the above variety until the acquisition of additional data.

During a collecting expedition in the autumn of 1928, the author encountered a large colony of these anomalous Amsonias near Bourbon, Missouri. Again in the spring of 1929 they were discovered near Hines and Gainesville, also in Missouri, the latter only a few miles north of the Arkansas state line. From these, as well as other observations in the field, the specific individuality of the plants appears quite evident. A description follows:

Amsonia illustris Woodson, n. sp.[2]

[1] Woodson, R. E., Jr. Studies in the Apocynaceae. III. Ann. Mo. Bot. Gard. **15**: 379–434. *figs. 1–3, pl. 50–53.* 1928.

[2] **Amsonia illustris** sp. nov., herbaceis perennis; caule erecto ramoso striato omino glabro 7–11 dm. alto; ramis erectis vel pauce ascendentibus; foliis alternis vel subverticillatis petiolatis membranaceis lanceolatis vel lineari-lanceolatis 5–7 cm. longis 1.0–1.5 cm. latis supra coriaceis illustris subtus glabris; lobis calycis hirsuto-strigillosis 1.5–3.0 mm. longis, triangulo-oblongolanceolatis; corolla salverforma puberula, tubo 6–8 mm. longo, limbo 5-partito 4–6 mm. lato; stigmate apice truncato; folliculis teretibus gracilibus continuis vel subtorulosis glabris sessilibus 8–14 cm. longis.—Missouri: collected along beds of gravelly branches near Webb City, July 15, 1909, *E. J. Palmer 2438* (Mo. Bot. Gard. Herb. type).

Issued December 30, 1929.

Herbaceous perennial from a somewhat thickened, woody rootstalk; stems terete, 7–11 dm. tall, 5–10 mm. in diameter at the base, 2–3 mm. in diameter at the inflorescence, glabrous, clustered from the base, erect, bearing scale-like cataphylls towards the base, branched above, the branches ascending, nearly erect, about the length of the main stem; leaves membranaceous, alternate or somewhat whorled below, numerous, ascending or spreading, lanceolate to linear-lanceolate, acuminate at both base and apex, narrowing almost imperceptibly to the short petiole, the blades 5–7 cm. long, 1.0–1.5 cm. broad, glabrous or somewhat glaucous beneath, coriaceous and shining above; inflorescence relatively large and dense, barely held above the foliage, pedicels .25–.75 cm. long; calyx 1.5–3.0 mm. long, hirsute-strigillose, the lobes triangular oblong-lanceolate; corolla salverform, caerulean blue shading to buff at the base of the tube, the tube 6–8 mm. long, 2–3 mm. in diameter, pubescent without, the lobes spreading or slightly ascending, oblong to oblong-lanceolate, acuminate at the apex, 4–6 mm. long; stigmatic-cap about as long as broad, stigma depressed-capitate; follicles continuous or subtorulose, 8–14 cm. long, 2–3 mm. in diameter, gradually acuminate, sessile, glabrous, 9–30-seeded; seeds 5–11 mm. long, truncate-oblong, variously pitted and wrinkled, cinnamon-brown.

Distribution: sand-bars and gravelly banks of streams, occasionally spreading into fields, Missouri, southeastern Kansas, eastern Oklahoma, and northeastern Texas.

Specimens examined:

MISSOURI: Moselle, July 2, 1886, *Eggert* (MBG); Webb City, gravelly branches, June 25, 1909, *E. J. Palmer 2339* (MBG); same locality, Sept. 2, 1909, *E. J. Palmer 2620A* (MBG, G); Gray's Summit, May 15, 1926, *Greenman 4493* (MBG); banks of the Meramec River, Minke, St. Louis Co., May 17, 1919, *Greenman 3944* (MBG); Webb City, common in woods, May 3, 1902, *E. J. Palmer 296* (MBG); same locality, common along beds of gravelly branches, July 15, 1909, *E. J. Palmer 2438* (MBG); Allenton, date lacking, *Letterman* (MBG); Spring Park, May 24, 1892, *Dewart* (MBG); Valley Park, St. Louis Co., May 15, 1897, *Trelease 459* (MBG); Franklin Co., July 2, 1886, *Eggert* (MBG); Carter Co., rocky banks, May 1, 1891, *Bush 966* (MBG); Carter

Co., May 1, 1891, *Mann* (MBG); Gascondy, July 21, 1914, *Emig 221* (MBG); Elmont, May 23, 1914, *Emig 250* (MBG); Jerome, June, 1913, *Kellogg 116* (MBG); Fox Creek, Allenton, June, 1880, *Letterman* (MBG, US); low ground, only two plants, south of Lee's Summit, June 3, 1917, *Hoffman* (MBG); chert barrens, Jasper Co., July 12, 1927, *Kellogg 1107* (MBG).

KANSAS: rocky soil, Allen Co., 1896, *Hitchcock* (MBG).

OKLAHOMA: on dry bank of draw, near Miami, Ottawa Co., Aug. 26, 1913, *Stevens 2337* (MBG, G, US).

TEXAS: swamps and low prairies, near Dallas, April 21, 1902, *Reverchon 3123* (MBG, G); Long Lake, Anderson Co., June 9, 1899, *Eggert* (MBG).

The abbreviations employed in the foregoing section refer as follows: MBG—Herbarium of the Missouri Botanical Garden; G—Gray Herbarium of Harvard University; US—United States National Herbarium.

Amsonia illustris constitutes a distinct addition to the subgenus Euamsonia by reason of several characteristics. It is the only species in the section with pubescent corollas which displays a hirsute calyx except *A. ludoviciana*, from which it differs in the texture of the leaves and follicles, geographical distribution, and additional particulars. The coriaceous and shining foliage, from which the species derives its name, is somewhat reminiscent of that of *Nerium Oleander* in shape and texture.

The follicles are unusually long, almost papery in texture, and are lax, sometimes even pendulous in position, an anomaly for the entire genus. The character that is most striking technically, however, is the construction of the follicles which are subtorulose: somewhat constricted between the seminiferous regions and inclined to dehisce immediately after maturity by breaking into several transverse sections. This character, however, is merely a suggestion of the condition of the follicles in the subgenus Articularia, and the follicles of *A. illustris* are in all important particulars typical for the subgenus Euamsonia. An additional anomaly of the follicles of the species is a tendency found in several specimens for only one carpel to develop, forming a single unusually stout and long follicle and bearing the sterile carpel as an inconspicuous basal protuberance.

Since the follicles of *A. illustris* are absolutely glabrous and otherwise unlike those of *A. ludoviciana*, its most pronounced affinity is with *A. Tabernaemontana* and its varieties, from which, however, it is readily separable by its hirsute calyx, its strikingly coriaceous, shining foliage, its scale-like cataphylls, which in the latter species are semifoliaceous, and its lax, subtorulose follicles.

A. illustris is a much more ornamental plant horticulturally than its relative *A. Tabernaemontana*, with which it has been cultivated in the author's garden for two seasons. Not only are the compact inflorescences more floriferous, but the habit of the plant itself is much more robust and compact, and the beautiful oleander-like foliage is almost evergreen. The foliage of the species is also somewhat reminiscent of that of the willow, which has occasioned the frequent identification by collectors as *A. salicifolia* Pursh (*A. Tabernaemontana* L. var. *salicifolia* (Pursh) Woodson).

PRELIMINARY STUDIES IN THE GENUS DALDINIA[1]

MARION CHILD

Jessie R. Barr Fellow in the Henry Shaw School of Botany of Washington University

Table of Contents

	Page
I. Introduction	411
II. History	413
III. Materials and methods	415
IV. Experimental data	417
A. Experiments in the germination of old ascospores	417
B. Experiments in the germination of fresh ascospores	422
1. Effect of oxygen	422
2. Effect of enzymes	425
3. Effect of ultra-violet radiation	427
4. Effect of temperature	431
5. Effect of different media	440
6. Effect of different hydrogen-ion concentrations	450
C. Factors influencing the growth of mycelium	456
1. Effect of light and darkness	456
2. Effect of different media and different temperatures	462
3. Effect of different hydrogen-ion concentrations	471
V. Morphological characters of the ascocarp and asexual stage of the forms studied	475
VI. Summary	476
VII. Acknowledgements	478
VIII. Bibliography	479

Introduction

The problem of fungous spore germination has not infrequently been the subject of physiological investigation, but many of the investigations have been carried on in the lower groups of fungi where the spores germinate relatively easily in comparison with those of the Ascomycetes, where germination is physiologically much more complex. It is only with a great deal of difficulty and after many types of experiments that germination is secured.

According to Saccardo ('82) and Ellis and Everhart ('92) there are in North America only four known species of *Daldinia.*

[1] An investigation carried out in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Science in the Henry Shaw School of Botany of Washington University.

These are *D. concentrica* (Bolt.) Ces. & De Not., *D. vernicosa* (Schw.) Ces. & De Not., *D. cingulata* (Lév.), and *D. loculata* (Lév.). Ellis and Everhart are of the opinion that *D. cingulata* is doubtfully distinct from *D. vernicosa,* but it seems to the writer that neither the descriptions of *D. cingulata* nor *D. loculata* are adequate. In this paper, however, the taxonomy of the group as a whole is not considered; the primary interest is a study of the factors influencing the germination of the ascospores and the growth of the mycelium of *D. concentrica, D. vernicosa,* and two undescribed species designated as *Daldinia X* and *Daldinia Y*.

As far as the writer is able to learn, a thorough study of ascospore germination of *Daldinia* has never been undertaken. Since the species *D. concentrica* is so widely distributed its ascospores have been observed and have been germinated in order that the life history of the fungus might be completely known. Its ascospores germinate rather readily in comparison with those of *D. vernicosa.* The ready germination of the ascospores of *D. concentrica* probably explains the fact that several workers have studied the fungus in pure culture. These workers have not, however, studied the influence of more than very ordinary factors on ascospore germination.

In striking contrast to the ascospores of *D. concentrica,* which germinate readily, are those of *D. vernicosa* which germinate only under very special conditions. Just as these two species are quite distinct morphologically, they are even more different physiologically.

In addition to the preceding species there are two as yet undescribed, *Daldinia X* and *Daldinia Y*. The former was collected in two different localities in Missouri and could not be classified among the described species of North America or even of foreign countries. It is, however, more closely allied to *D. vernicosa* than to *D. concentrica.* It differs, however, from *D. vernicosa* in size and color of ascocarp and ascospores. *Daldinia Y,* a species from the Black Hills of South Dakota, apparently is more closely related to *D. concentrica* and was so named in the herbarium of the Missouri Botanical Garden. It differs from the typical species by size and markings of the ascocarp, and in the size and color of the ascospore. In both of these undescribed

species the morphological differences are completely correlated with physiological ones.

In view of the fact that the distribution of *D. concentrica* is so universal and also since so many forms have been included in the species, it seemed desirable to the writer to study this species not only from the morphological but from the physiological point of view, for environmental conditions may so completely modify a species that uncritical investigators may be led to the wholesale creation of new species. It seemed fitting that a more modern attitude should be taken and that morphological characters should be correlated with physiological characters as shown by pure culture. By adopting such an attitude, it is possible not only to obtain a clearer conception of a species but also to determine its biological reactions.

Further investigations concerning the cytology and taxonomy of the ascigerous stage of North American material are under way.

History

There are, as far as the writer is able to learn, only eight investigators who have published studies of *Daldinia*. Only three of these investigations were published as separate and special studies, the others merely being a result of work done in a large group of which *D. concentrica* was a member. *D. concentrica* with one exception was the only *Daldinia* studied in pure culture. The majority of investigators merely observed the ascocarp, ascospores, and conidia, in the natural habitat.

Among the first investigators were the Tulasnes ('63), who published a description of the ascocarp and also noted in the natural habitat the presence of conidia on the ascocarp previous to the formation of perithecia. Twenty-eight years later Brefeld ('91) described the ascocarp in its natural habitat and also observed ascospore germination.

As part of an investigation of the fungi of Brazil, Möller ('01) made observations on the biology of the fungus. He observed the rapidity of the growth of the stroma and the duration of ascospore production in the natural habitat. From the germinated ascospores he obtained the conidial stage in culture. Information as to media and methods is insufficient.

The first worker to make a special study of *D. concentrica* was Molliard ('04), who studied particularly the conidial stage in order to assign it a definite taxonomic position and name. Germination of the ascospores was obtained after three days at 15° C. on slices of carrot, and on other media which were not stated. In observing the development of the mycelium, changes in color and the development of nodular tufts were noted, the nodular tufts being reminiscent of the stroma of the perfect stage. Conidia were at first obtained after two months, but in later experiments were observed to appear within two or three weeks. They were noted to be ovoid, almost colorless, 7–8 μ long × 4.5–5.4 μ wide, and pointed at the end where they were attached to the little sterigmata-like base. For the conidial stage he proposed the name *Nodulisporium Tulasnei*.

A few years later Brooks ('13) published the results of some experiments with the Ascomycetes and Basidiomycetes. In this paper there is reference to his obtaining from germinated ascospores of *D. concentrica*, conidia in pure culture. *Fraxinus* wood blocks sterilized in tubes, the bottoms of which held plugs of water-saturated cotton were used as a medium. The cultures were placed in dull light at room temperature, and the resulting mycelium, which was at first white, became tawny with age and where coming in contact with the glass became blackened, aggregated so that it resembled the hyphae which formed the matrix of the stroma. The conidiophores were branched and from them elliptical hyaline spores, 6–8 × 3–4 μ, borne singly and in heads, were abstricted. The hyphae readily penetrated the wood and were especially abundant in the vessels.

One of the more recent workers on *Daldinia* is Elliot ('20) who studied the formation of conidia and the growth of the stroma. With conidia from the natural habitat *Fraxinus* blocks were inoculated, then placed in the open on the ground. *Fraxinus* chips were inoculated and kept in the laboratory. Although she did not clearly distinguish between results with pure culture and those in open air, it is evident that most of the observations were made on the material in the open air. Ascospores germinated on the exterior of the ascocarp and in the perithecia when kept in a damp condition under a bell jar, and the mycelium thus pro-

duced gave rise to conidia in a few days. The conidial form under natural conditions appeared as a cream-colored incrustation of conidiophores that were much branched in a verticillate manner and terminated in clusters of hyaline conidia. For the most part the discussion is given over to the perfect stage.

Following the investigations of Miss Elliot are those of Miller ('28), who has studied the biology of the *Sphaeriales* and in this group has included some investigations on *D. concentrica*, *D. Escholzii*, *D. vernicosa*, and *Hypoxolon placentiforme*, noting that in all forms the conidial layer is a light grayish-brown, that the conidia are hyaline with a slight greenish tint, are 6–8 μ long × 4–5 μ wide, and are borne on sympodially branched conidiophores. No work was done on spore germination.

The last paper concerning *Daldinia concentrica* has been published by Panisset ('29), who identified this fungus as the one which commonly attacks *Fraxinus excelsior* and causes an irregular brown to black coloring known to timber merchants as "calico wood." In order to identify this fungus she germinated the ascospores on various solid and liquid media, observed mycelia and the discoloration of the medium resulting from the germination of the conidium, finding that the discoloration agreed with that resulting from the germination of the ascospores and with the hyphae and brown staining in the calico wood. The external conditions of growth as regards water, oxygen acidity and alkalinity, the food materials utilized by the fungus inside the wood, and the nature and production of the brown substance were investigated.

Materials and Methods

These studies were chiefly with pure cultures isolated from collections made by the writer in Pulaski County, Missouri; by Dr. Linder in Missouri, and Canton, Massachusetts; and with material from the herbarium of the Missouri Botanical Garden.

In all except a few cases ascospore germination was studied in hanging-drop or van Tieghem-cell cultures. The ascospores, directly from the freshly cut perithecia, were placed on the medium by means of a sterile platinum needle. Unless otherwise indicated, the ascospore cultures were always put into a dark

cabinet of approximately room temperature, for better germination was secured in the dark than in the light. When a liquid medium was used as a source of nutrition, three or four drops of the same solution were placed in the bottom of the cell in order to insure equilibrium within the cell and thus to prevent changes in the concentration of the solution. When a solid medium was used the nutrient solution minus the agar was placed in the bottom of the cell. This also served as a source of the necessary moisture. All cultures both in the study of spore germination and mycelial growth were made in duplicates or triplicates; frequently erratic results necessitated repetition as many as ten times. Spore counts were made under low and high power of the microscope. Two hundred ascospores from different fields were counted in each Van Tieghem cell and then an average taken. The tables not only include the results of the individual experiments, but the averages of them. This was done in order to show the occasional erratic behavior of the fungus. The graphs are based upon the average of a stated number of experiments which will be indicated in each case. In both the tables and the graphs the discussion is based upon the average.

The isolation of the fungi for experiments on mycelial growth was made by the single-spore method of Kauffman, with one exception, *Daldinia Y* (Black Hills, South Dakota), in which case the material was twenty-five years old and the ascospores would not germinate under a variety of conditions. In this case the isolation was made by washing the surface of the ascocarp with a 70 per cent solution of ethyl alcohol, then with a sterile knife a piece of the stromatic material was cut out and dropped into a few cc. of sterile distilled water to which had been added a few drops of 10 per cent lactic acid. After a thorough shaking, the material was put into an abrasion on the agar plate.

With few exceptions all of the observations made on mycelial growth were from cultures in petri dishes, which had been inoculated with ¾–1 sq. cm. of actively growing material of the same age. The radial growth was measured from the periphery of the inoculum to the periphery of the colony; the first measurement was made two days after the plates were inoculated and the second measurement a few days later, before the mycelium had

covered the surface of the medium. The rate of growth per day was then calculated by subtracting the first measurement from the second and dividing by the number of days which intervened. This was done in order to obtain more accurately the rate of growth per day, thus averaging rapid growth which might occur due to mycelium stored with food products, and growth which was slight at first due to relatively little stored food products.

For germination, both solid and liquid media were used, but for the study of mycelial growth, solid media only. Among the latter are oatmeal, Leonian, Pfeffer (Fe omitted), prune, *Tupelo* sp., and *Platanus occidentalis* L. decoction agars, prepared according to the regular formulae. For hydrogen-ion work, Pfeffer's solution as prepared by Gillespie ('18) with the addition of 3 per cent agar was used; the solutions were made acid by citric acid and basic by NaOH. They were tested by the colorimetric method before and after sterilization.

Experimental Data

Experiments on the Germination of Old Ascospores

In these experiments herbarium material from the Missouri Botanical Garden and fresh material from other sources were used. The herbarium material included three different collections of *D. concentrica* from Missouri, one from the Black Hills of South Dakota, one from Alabama, and two from the Philippine Islands, and one, *D. vernicosa,* from Missouri. The fresh material used in the latter part of this study included *D. concentrica*, *D. vernicosa*, and *Daldinia X* from Missouri. One *D. vernicosa* came from Canton, Massachusetts.

The names of the fungi, the places where they were collected, and the age will hereafter be abbreviated as follows:

Herbarium material:

D. concentrica Philippine Isl. 16 yrs. old—*D. concentrica* (No. 12465)

D. concentrica Philippine Isl. 12 yrs. old—*D.* concentrica (No. 59960)

D. concentrica Meramec, Mo. 23 yrs. old—*D. concentrica* (No. 16363)

D. concentrica Auburn, Ala. 3 yrs. old—*D. concentrica* (No. 16365)

D. concentrica St. Louis, Mo. 32 yrs. old—*D. concentrica* (No. 43049)

D. vernicosa Lesterville, Mo. 2 yrs. old—*D. vernicosa* (L. Mo.) (No. 63847)

D. vernicosa Canton, Mass. 3 yrs. old—*D. vernicosa* (C. Mass.)

Daldinia Y Black Hills, S. Dak. 25 yrs. old—*Daldinia Y* (B. S. D.) (No. 43121)

Fresh material:

D. concentrica Dixon, Mo.—*D. concentrica* (D. Mo.)

D. vernicosa Dixon, Mo.—*D. vernicosa* (D. Mo.)

Daldinia X Valley Park, Mo.—*Daldinia X* (V. P. Mo.)

At first various attempts were made to secure germination with two-year-old ascospores of *D. concentrica* (D. Mo.) but without success. Tap water and distilled water were of no value, and although Stevens ('98) found that ethyl and methyl alcohol in different normalities acted as specific stimuli to the spores of various fungi, this treatment also failed. By soaking the ascospores of *D. concentrica* (D. Mo. 2 yrs. old), *D. vernicosa* (L. Mo.), and *Daldinia Y* (B. S. D.) in ethyl alcohol for different lengths of time up to a week, then putting them into weak sucrose solutions, the spores merely swelled and did not germinate. The ascospores of *D. concentrica* (D. Mo.) and of *Daldinia Y* (B. S. D.) swelled more than those of *D. vernicosa* (L. Mo.) and *D. vernicosa* (C. Mass.). When weak sucrose solutions of 1–10 per cent seemed to induce swelling, additional percentages were tried. However, 20 per cent solution caused plasmolysis and no germination.

All of the ascospores were observed to have hyaline exospores, which in any of the fresher *D. concentrica* sloughed off under moist conditions, while in the older material they cracked off irregularly. The exospores were about .07 μ and were stained by the lacto-phenol-cotton-blue mounting medium. The apparently chitinized amber-colored wall which remained after the hyaline exospore sloughed off was very thin. The hyaline exospores of *D. vernicosa* were only about 105 μ thick and did not take the stain of cotton-blue in lacto-phenol as well as did those of *D. concentrica*. The chitinized amber-colored wall of the former was heavier than that of the latter species. In fresh material the exospore of *D. concentrica* under moist conditions sloughed off

about five hours after the culture was made up but soon disappeared by dissolving in the medium. In only a few cases have exospores of *D. vernicosa* been observed while sloughing off. The exospore ruptures irregularly, never regularly as in fresh material of *D. concentrica,* and probably also dissolves in the medium.

Some investigators have observed that the "spore pellicle" or exospore must be dissolved or cracked off before germination will occur. Hartig ('85) found that ammonia or some alkali was necessary for dissolving the "spore pellicles" of *Merulius lachrymans* before germination would occur. This does not seem to be necessary in *Daldinia,* but it does seem necessary to dissolve or break down the amber-colored chitinized spore wall. In attempting to rupture this wall, the ascospores were ground on a rough glass by means of a scalpel, then placed in a small quantity of sterile distilled water to which a few drops of a 10 per cent solution of lactic acid were added, or different percentages of alcohol or sucrose or wood decoctions. The hyaline exospores were cracked off irregularly by this mechanical means, but the walls of the spores were not affected, and no germination occurred.

Whether the spores needed a stimulus or a perfect source of nutrition, or both, had to be determined. Since the fresh material had not been fumigated, the spores might still be viable, and would germinate if the correct nutrient were found. Some standard agar medium, oatmeal, Pfeffer, Pfeffer with the addition of sucrose, string-bean, and prune decoctions, was tried. All of the above-mentioned herbarium material and material from other sources were used. The ascospores of *D. concentrica* (Nos. 16363, 16365, 43049) on all of the media showed irregularly cracked exospores and a slight swelling, but no germination after 120 hours, which time shall be taken as the limit although the cultures were run for two weeks. In the media where there was a high sugar content, swelling was in most cases more pronounced, always more so in *D. concentrica* than in *D. vernicosa.* The exospores of *D. concentrica* (Nos. 12465 and 59960) cracked from one apex to the other in a characteristic manner after 120 hours on prune-decoction and on Pfeffer-solution agar to which sucrose had been added. In some cases the hyaline exospore became roughened

but did not crack off. On other agar media the character of the spores did not change appreciably. When alternately shocked by dry freezing in an electric refrigerator at − 5° C. for two days, then heated in an incubator at 40° C. for the same length of time after which the ascospores were put on the different media, the exospores cracked from one apex to the other. Some ascospores on prune-decoction agar and Pfeffer-solution agar to which sucrose had been added cracked open longitudinally, due probably to the combination of heating, freezing, and high sugar content of the media. In no case did germination occur. When the ascospores were frozen they seemed to shrink, but upon heating regained their normal size.

The ascospores of *Daldinia* Y (B. S. D.) became considerably swollen and the oil globules became more pronounced in a 20 per cent sucrose solution, but plasmolyzed after 48 hours. On prune-decoction agar the exospores sloughed off irregularly and the oil globules also became larger. In some cases the ascospores cracked open, due probably to the high osmotic pressure which results from a medium of high sugar content.

Since *D. vernicosa* is frequently found on charred logs, it was suggested that heat might play some part in germination; therefore the spores were heated by putting them in a small vial which was partially immersed in a double boiler, in which the water was allowed to boil for a few minutes. The ascospores of *D. vernicosa* (No. 63847) were then put on the different media, but in no case did they germinate, although the spores were slightly swollen and the exospores roughened. Maneval ('26) studied eight different species of rust teliospores and found that physiologically the spores changed during the winter. A sort of "ripening" occurred, for as the spring approached the percentage of germination in a given species requiring a rest period increased gradually to a maximum and then declined. As the time of maximum germination approached the time necessary for germination to start decreased to an hour or less. Since overwintering is considered a factor of real significance in the germination of fungous spores, an artificial means of overwintering was employed here by freezing the spores in a refrigerator. The ascospores were put into small vials containing a few cc. of sterile

distilled water and frozen for a week at – 5° C. After that time the ice was melted and the ascospores were sprayed on a plate of oatmeal agar. Some of the ascospores cracked open, while others swelled slightly, but again there was no germination. Ascospores of *Daldinia Y* (B. S. D.) when treated alternately with freezing and heating did not swell; the exospores cracked off irregularly, but there was no germination. As in the preceding the exospores of *D. vernicosa* (C. Mass.) were observed to be cracked off after having been heated, but in the controls the exospores were in the majority of cases not even roughened. When on a medium with a high sugar content, the ascospores swelled considerably but by no means to the same extent as in *D. concentrica*. Other media gave no better results. Alternate dry freezing and heating caused a cracking open in most cases, but two or three ascospores of *D. vernicosa* (C. Mass.) germinated out of thousands that were in the cultures. These ascospores were kept under observation for a month, but for no apparent reason their development was soon arrested (pl. 37, fig. 4).

Although it is known that some fungous spores remain viable over a period of many years, even after fumigation, it is quite obvious from the results of these experiments that the viability of these ascospores is seriously affected either by age or disinfectant (in this case CS_2). Nevertheless in spite of negative results it is apparent that the ascospores of *D. vernicosa* are much more resistant than those of *D. concentrica* and its relative, *Daldinia Y* (B. S. D.). This has a direct bearing on the interpretation of the later results.

The preceding experiments show that water and alcohol have little effect on such old ascospores. Grinding merely cracked off the exospore and did not affect the chitinized wall. The older material showed a more irregular cracking off of the exospore than the fresher material. Certain concentrations of sucrose, prune-decoction agar, and Pfeffer-solution agar to which sucrose had been added caused plasmolysis and even a bursting open of the ascospore. Alternate dry freezing and heating might also have the same effect. Short periods of heating alone have little effect, but in one case freezing induced a very small percentage of germination of *D. vernicosa* (C. Mass.) ascospores.

Experiments in the Germination of Fresh Ascospores

In the experiments which follow, fresh material of *D. concentrica* (D. Mo.), *D. vernicosa* (D. Mo.), and *Daldinia X* (V. P. Mo.) only was used, since most of the results of the preceding experiments gained from old material were negative.

EFFECT OF OXYGEN

In attempting to determine one of several factors which evidently influence germination of ascospores, an excess of oxygen was tried in order to determine whether or not the oxygen supply was a factor in the germination of *Daldinia* ascospores. DeBary ('87) stated that oxygen for the germination of fungous spores had never been sufficiently demonstrated and that perhaps spores germinated only after the oxygen in the drop culture had been exhausted. There are investigators who have proved the necessity of oxygen for germination. Maneval ('26), for example, has found that for the germination of teliospores of the rusts the oxygen supply is a very important factor. Reed and Crabill ('15) found that oxygen was apparently necessary for the germination of *Gymnosporangium Juniperi-virginianae*, and that the carbon dioxide of the atmosphere prevented germination. That a scanty oxygen supply prevented the germination of the spores of *Plenodomus fuscomaculans*, Coons ('16) was able to demonstrate.

In the first oxygen experiment small amounts of the alga *Pleurococcus* sp., were put in the bottom of the van Tieghem cells containing distilled water. The cover glasses were only lightly put on the cells in order to allow some circulation of air. Then the cells were put in a window where the light was abundant. After two days, more water was added and the spore inoculations were made on Pfeffer agar. Slightly better germination of *D. concentrica* in cultures in which the alga was used was obtained than in the controls. After 96 hours 80 per cent germination was secured, while in the controls 78 per cent. The only other difference in germination was a more profuse branching of the mycelium in the cultures containing the alga than in the controls. The ascospores of *D. vernicosa* germinated slightly better in the controls than in the cultures where the alga was used. After

96 hours 61 per cent germination was secured, while in the controls 10 per cent. The ascospores in the cultures with the alga swelled more, became a lighter brown, and had longer germ-tubes than those in the controls. It would seem from these results that an abundance of oxygen accelerates growth of the germ-tubes in both cases, but does not increase the percentage of germination in *D. vernicosa.*

The second means of obtaining an extra supply of oxygen was a 3 per cent solution of hydrogen peroxide, which was used as a medium and as the liquid in the bottom of the cell; the slight trace of alkali in the glass and the light cause the decomposition of hydrogen peroxide with a release of oxygen. After 120 hours the ascospores of *D. concentrica* and of *D. vernicosa* in hydrogen peroxide had not germinated. After 24 hours the ascospores of *D. concentrica* had swollen slightly and had become a lighter brown. The ascospores of *D. vernicosa* had become considerably swollen and the natural brownish-black color which is so characteristic of mature *D. vernicosa* spores had become a light brown, due to an oxidizing process. Ordinarily the spores retain their dark brown color even after germination. Since no germination was secured when the spores were put into the hydrogen peroxide, Pfeffer agar was used as the medium with hydrogen peroxide in the bottom of the cell. No germination was obtained in *D. concentrica* where hydrogen peroxide was used, although in the controls it did occur. The ascospores of *D. vernicosa* in hydrogen peroxide germinated poorly; the spores although considerably swollen were evidently oxidized. The germ-tubes were short, very wide, and very granular. Germination however poor was slightly better in the controls, and the short germ-tubes were less granular.

Since these methods of supplying oxygen proved inaccurate, an oxygen tank was employed. From a small tank of 40-gallon capacity a slow stream of oxygen was allowed to pass into a large water-filled bell jar suspended in a cylinder of water. As the oxygen passed out into the bell jar the water passed into the cylinder and the bell jar rose. After considerable experimenting a steady stream from the tank balanced the stream out of the bell jar, but this stream could not be maintained for more than

six hours. By clamps on the tubing leading from the tank to the bell jar and from the bell jar to the first tower, the stream of oxygen was regulated. From the bell jar the oxygen went through a tower of KOH, then through a gas-washing bottle containing a saturated solution of $Ba(OH)_2$; thus there was a double check for the elimination of CO_2. On a wooden rack the height of the stage of the microscope a series of Wardian cells, the same size as the van Tieghem cells, was mounted on slides by means of balsam. These cells were supplied with glass inlets and outlets 6 cm. long and 3 mm. in diameter. The hanging-drop method was used with Pfeffer agar as the medium, then the cover glasses were cemented to the cells by carefully applying a mixture of beeswax and paraffin. Since this cement would not withstand the pressure of the flow of oxygen, weighing bottles containing about 10 cc. of mercury were put on top of the cells, after the beeswax-paraffin preparation had been applied. From the cells the oxygen passed into a shallow cylinder of water and the bubbles counted here were used as an indication of the number of bubbles per minute that passed through the cultures. All the connections were carefully sealed with shellac in order to insure a leak-proof system. The apparatus was set up in a dark-room at a temperature of approximately 24° C. To examine the cultures the cells were carefully moved onto the stage of the microscope. No detachment was necessary since the rack was open at both sides and the microscope light could be moved along freely with the microscope. After some experimenting it was found necessary to divert the flow of oxygen through Y-tubes then into the cells in order to secure a steady flow of oxygen. A constant flow of oxygen of 68 bubbles per minute for six hours was maintained with only six cells in two parallel rows connected by Y-tubes of 5 mm. in diameter.

The results of these tests indicate that ascospores of *D. concentrica* supplied with oxygen from the tank germinated slightly better than the ascospores in the controls. The ascospores treated with oxygen did not swell as much as those not treated, but their exospores sloughed off and disappeared sooner. The flow of oxygen may carry the ascospores away or they may be absorbed by the medium more quickly than when not treated

with oxygen. In almost all cases, the germ-tubes of the oxygen-treated ascospores were very bulbous at the base of the spore. This may be due to a sudden germination. In both the oxygen-treated ascospores and the controls, germination occurred in less than 24 hours. Spores frozen in a dry state for a period of two months and non-frozen spores were used in the oxygen experiment. In cultures where non-frozen ascospores were used, the percentage of germination was higher and the spores were more swollen than in cultures where frozen spores were used. Dry frozen and non-frozen ascospores of *D. vernicosa* and *Daldinia X* germinated slightly better in the controls than in cultures with an excess of oxygen supply, but the ascospores of the latter were lighter brown and the germ-tubes were more granular and more swollen than were those in the controls. Therefore it seems that oxygen in excess does not increase the percentage of germination in *D. vernicosa* but it does slightly in *D. concentrica*. While an excess of oxygen causes only a slight change in color to the ascospores of *D. concentrica* and less swelling than in the controls, considerable swelling is induced and a change from a dark brown to a light brown color is observed in oxygen cultures of *D. vernicosa* ascospores. In both species the growth of mycelium is accelerated by the excess supply of oxygen. Ascospores of *Daldinia X* were also treated with an excess supply of oxygen, but they were apparently indifferent for no better germination was secured than in the controls.

EFFECT OF ENZYMES

Even though the species of *Daldinia* are not dung-inhabiting or obviously dependent upon some enzyme as a stimulus to ascospore germination, enzymatic activity might be a factor in germination, for the presence of slugs in freshly formed ascocarps of *D. concentrica* and *Daldinia X* has been frequently noted. Since in the writer's experience *D. vernicosa* has been found only once infested with slugs, it is suggested that the rarity of its occurrence may in some way be correlated with a lack of external enzyme activity.

Boudier ('69) believed that the spores of species of *Ascobulus* growing on dung germinated only after passing through the

digestive canals of animals and that the spores of species growing on the earth germinated at ordinary temperatures without special treatment. Janczewski ('71) proved that the spores of *Ascobulus furfuraceus* germinated readily after having been recovered from the faeces of an animal. The epispore was removed during the digestive process, indicating that enzymatic activity was essential to germination. There are others[1] who have successfully germinated spores in dung decoctions or have by other artificial means supplied the necessary enzyme for the dissolving of the exospore. A most interesting bit of work by Fraser ('07) on spore germination was the imitation of normal digestion which occurred when spores were placed in saliva, artificial gastric juices, pancreatic juice, and dung decoction. She found that the alkalinity supplied by the dung decoction was one of the two most important factors in germination, the other factor being heat.

One of the early investigators of spore germination was Hoffman ('60), who employed a solution of HCl and pepsin as a stimulus to germination of basidiospores, but he found that poor germination occurred. Ferguson ('02) used pepsin, distilled water, and HCl in different concentrations to stimulate spores of certain Agarics to germinate, but germination was so erratic that no conclusions could be drawn. She did find, however, that when the spores of *Agaricus campestris* came in contact with the actively growing mycelium perfect germination was secured in 144 hours, due to the secretion of an enzyme from the mycelium. Jahn ('05) has said that in the process of spore germination of the Myxomycetes the cell wall ruptures by pressure from within, but an enzyme "glycogenase" also plays a part in the process by changing the glycogen in the spore to maltose, and, since the osmosis-producing material in the newly arising protoplasm is a sugar, promotes germination. As has been asserted by Constantineau ('06), the germination process of myxomycetous spores is independent of osmotic pressure, and from a comparison of germination in isotonic solutions germination is dependent upon the ability of the spores to utilize the sugars. A more recent worker, Skupienski ('22), maintains that germination of myxomycetous spores is a purely osmotic phenomenon and not due to any enzyme activity. The most illuminating

[1] Van Tieghem ('76), Ternetz ('00), Massee and Salmon ('01, '02).

work on this subject has been done recently by Gilbert ('28), who studied 56 species and varieties of myxomycetous spores germinating in distilled water. He observed two distinct types of germination: 1, by internal pressure as exemplified by the sub-order Calcarineae; and 2, probably by enzyme action, as exemplified by the order *Lamprosporales*.

The writer employed aqueous pepsin solutions of 10, 5, 2, 1, 0.5, and 0.1 per cent, in the hope of stimulating ascospore germination. The ascospores of *D. concentrica*, *D. vernicosa*, and *Daldinia X* were placed in these different solutions, but germination did not occur in any of them and the spores did not even swell except in the 5 per cent solution. The results were no more favorable when the ascospores were subjected to actively growing mycelium. The results of both of these experiments were in contrast to those of Miss Ferguson, since the spores of none of the species were influenced to greater germination. Unfortunately, the writer could pursue no further this phase of the work on enzyme activity, but it is hoped that at a later date a more complete account may be given.

EFFECT OF ULTRA-VIOLET RADIATION

While the writer was raying cultures of mycelium, it was suggested that ultra-violet rays might stimulate germination. Stevens ('28) has observed the lethal effect of ultra-violet radiation on conidia of *Glomerella cingulata* (Stoneman) Spalding and von Schrenk strain G. 10. He used full radiation from a Cooper-Hewitt quartz mercury arc operated at 4.5 amperes and 66 volts, with the petri dishes 21 cm. from the light. With the conidia on the surface of cornmeal agar, exposure for 5 seconds caused poor germination, 10 seconds, poorer germination, and after 15 seconds or more there was none. When the conidia were protected by 1.5 mm. of cornmeal agar, under exposure 5, 10, and 15 seconds poor germination followed; after exposure of 20, 25, and 30 seconds germination was only fair; 35, 40, and 45 seconds gave poor germination; 60, 70, 80, and 90 seconds gave very poor germination. The lethal effect therefore lies at slightly more than 90 seconds.

In the writer's experiments the lamp used for raying was an air-cooled Uviarc quartz lamp from Burdick Cabinet Co. The

only screen used was Vita glass from Hires Turner Glass Co. When this screen was used the rays allowed to pass were between 578 and 289 μμ (5780 A.U.—2894 A.U.).

The van Tieghem cells were prepared in the usual manner for germination experiments, and Leonian agar was used as a medium on which the ascospores, directly from the perithecia, were placed. For raying, the cover glasses with the medium and spores were carefully turned right side up and the slides were placed under the Vita glass box. After exposure, water was added to the cells, to which the cover glasses were then cemented by means of vaseline. The cultures were put in the dark and subsequently examined for germination at the end of 24 and 48 hours. All cultures were rayed for 25 seconds at 70± volts, and 42 cm. from the lamp. The results are given in table I.

TABLE I

GERMINATION OF ASCOSPORES SHOWING THE EFFECTS OF FREEZING AND ULTRA-VIOLET RADIATION. FOR EACH SPECIES AND EACH TREATMENT, 800 SPORES WERE COUNTED. LEONIAN AGAR WAS USED

Fungus	Treatment	Percentage of germination					
		Rayed			Not rayed		
		Experiments			Experiments		
		1	2	Average	1	2	Average
D. concentrica (D. Mo.)	Frozen*	95.0	83.0	89.0	87.0	69.0	78.0
	Not frozen	99.0	88.0	93.5	93.0	70.0	81.5
D. vernicosa (D. Mo.)	Frozen	2.0	2.0	2.0	4.0	4.0	4.0
	Not frozen	0.0	3.0	1.5	0.0	2.0	1.0
Daldinia X (V. P. Mo.)	Frozen	0.0	0.0	0.0	0.0	1.0	0.5
	Not frozen	0.0	0.0	0.0	1.0	0.0	0.5

* Dry ascospores frozen 2.5 months at −5° C.

This experiment with three-months-old material was divided into two phases: one in which the ascospores had been previously frozen, the other in which the material was not treated before raying. Controls were used in both cases. The percentage of germination of frozen spores of *D. concentrica* was lower in the controls (78 per cent) than in those not frozen (81.5 per cent).

While the relative germination remained proportionately the same, there was a slight increase in the percentage of germination in both groups after raying, namely 89 per cent for the frozen, and 93.5 per cent for the untreated material. *D. vernicosa*, on the other hand, reacted in quite a different manner. Freezing of the spores favored germination in the rayed and non-rayed material in this case, but the ultra-violet light inhibited spore germination. It should be noted that when the spores were not frozen and were rayed, there was a significant improvement in germination. Why this was the case is difficult to determine, although it might be that raying has much the same effect as freezing and might stimulate germination, while the ascospores which have been frozen as a result of their treatment have been made more susceptible to the action of the rays. This view seems to be supported by the fact that the rayed ascospores that did not germinate were more swollen than those not rayed. While the preceding hypothesis may hold true, there is also the possibility that the difference of .5 per cent may be laid to experimental error or irregularity in germination, yet in view of the large number (9600) of spores counted such could hardly be the case. The spores of *Daldinia X*, while germinating very poorly, were apparently little affected by freezing, although raying resulted in no germination at all.

From the above it is evident that these three species have distinct physiological reactions, and that raying, while beneficial to the ascospores of *D. concentrica*, is harmful to those of the remaining two species. Also it is clear that germination of the ascospores of *D. concentrica* is impeded by freezing, while the spores of *D. vernicosa* are favored. In general the rayed ascospores produced heavier and more frequently branched germ-tubes than did the controls, in which event it would seem that the ultra-violet rays, in the dosage used, act as a stimulus to growth.

When dry freezing of ascospores of *D. vernicosa* was observed to stimulate germination, it was suggested that even longer periods of freezing might be more effective. Hence after three months at – 5° C., cultures of *D. concentrica* and *D. vernicosa* and *Daldinia X* were made, using Pfeffer agar as the medium. Observations made after 48 hours still further confirmed the

previous evidence that freezing has a deleterious effect on the ascospores of *D. concentrica*. There was from 5 to 10 per cent more germination in the controls than in the cultures in which the frozen spores were used. The ascospores swelled considerably, as is characteristic, but the unfrozen ascospores were swollen more than the frozen ones. The germ-tubes of the unfrozen ascospores were long and unbranched, while those of the frozen ascospores were short with one to three short branches. The mycelium was heavily granular, indicating slower growth. In *D. vernicosa* 10 to 15 per cent more germination of the frozen ascospores was secured than of the controls. This is the most illuminating evidence that freezing is a stimulus to germination in this species, for in no previously tried stimuli has such a high percentage of germination been obtained. The character of the spores and germ-tubes in the culture where frozen spores were used was not significantly different from that in the controls. A third physiological reaction as represented by *Daldinia X* differs from the other two specific reactions by only a slight increase (1 to 1.5 per cent) in germination of the frozen spores over those of the controls. It would seem that this species is rather indifferent to freezing as far as the character of the ascospores and germ-tubes is concerned, for in both cases they are practically the same.

Why the ascospores of the three species should respond to freezing in so diverse a fashion is difficult to explain except that the physiological constitution of each is quite distinct. Freezing of the ascospores of the two species favorably stimulated might cause chemical changes in the ascospores, and as a result it is quite possible that the condition of the protoplasm is altered or some constituent not previously capable of being utilized may be made available by this treatment. Another possibility is that a low temperature might favor the action of some enzyme that renders reserve material available for the metabolism of the spore, preceding actual germination. Freezing may also reduce the water content of the ascospores so that the greater osmotic pressure inside may alter the permeability of the ascospore wall.

EFFECTS OF TEMPERATURE

It is evident from the preceding results that ascospores more than a year old will germinate only poorly even under a wide variety of conditions or will not germinate at all, while ascospores from one to four months old will germinate rather readily, the percentage of germination depending on the species and on the environmental factors. It is due to this fact that old material was not used in these further experiments intended to determine the factors favoring germination.

EFFECTS OF HIGH TEMPERATURES

One of the most important factors in ascospore germination of *Daldinia* is temperature. That temperature is a factor of consequence in the germination of other fungous spores has been shown by Haberlandt ('78), Müller-Thurgau ('85), Eriksson ('95), and others, who found that the subjection of the ascospores to cold for longer and shorter periods improved germination and favorably affected other life processes. That a high temperature may take the place of a food or may be the only necessary stimulus to germination is claimed by Ferguson ('02) in the case of *Hypholoma appendiculatum*. When she subjected the spores to 28° C.±, and bean decoction and distilled water were used as media, 90 and 75 per cent respectively of the spores germinated, while at 16° C. ± no germination was secured. That high temperatures for short periods of time are effective as a stimulus to germination of ascospores of *Daldinia* will be seen shortly.

When temperatures from 70 to 100° C. were employed, a double boiler containing water in both parts of the vessel was used. From a ring stand at the side of the vessel a thermometer and a small wire basket were suspended in the water of the upper part of the boiler. Under the double boiler a carefully regulated flame was maintained. The heating operations were carried on in a hood in order to avoid drafts which would prevent the maintenance of a constant temperature. The small wire basket was divided into two portions by cross wires, and small cork-plugged vials containing bits of stromatic material and perithecia were put into the basket which was lowered into the water half way up the sides of the vials. For each exposure different bits of

material from the same collection were used. Ascospores were then taken from the treated perithecia by means of a platinum needle and the usual hanging-drop culture was employed with Pfeffer agar as the medium. Ascospores of *D. concentrica* and *D. vernicosa* five months old were used in these experiments, the results of which, shown in tables II and III, represent a count of 25,400 ascospores of each species.

TABLE II

D. CONCENTRICA (D. MO.)

PERCENTAGE OF GERMINATION OF ASCOSPORES SHOWING THE EFFECT OF SHORT EXPOSURES TO HIGH TEMPERATURES. EACH EXPOSURE AND PERIOD REPRESENT A COUNT OF 600 SPORES. PFEFFER AGAR WAS USED

Temp. ° C.	After 24 hrs.				After 48 hrs.			
	Experiments							
	1	2	3	Av.	1	2	3	Av.
	Exposure of 15 minutes							
100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
95	0.0	0.0	0.0	0.0	0.0	3.0	0.0	1.0
90	0.0	26.0	0.0	8.6	1.0	30.0	0.0	10.3
85	18.0	38.0	0.0	18.6	50.0	52.0	0.0	34.0
80	1.5	45.0	4.0	16.8	4.0	49.0	7.0	20.0
75	52.0	0.0	7.0	19.6	57.0	18.0	15.0	30.0
70	30.0	30.0	34.0	31.3	75.0	65.0	40.0	60.0
	Exposure of 10 minutes							
100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
95	2.0	3.0	0.0	1.6	17.0	16.0	0.0	11.0
90	2.0	1.0	0.0	1.0	13.0	5.0	0.0	6.0
85	1.5	25.0	0.0	8.8	25.0	33.0	0.0	19.3
80	50.0	49.0	5.0	36.6	56.0	54.0	10.0	40.0
75	0.0	0.0	0.0	0.0	0.0	19.0	0.0	6.3
70	20.0	50.0	17.0	29.0	22.0	54.0	22.0	36.0
	Exposure of 5 minutes							
100	0.0	0.0	0.0	0.0	4.0	0.0	0.0	1.3
95	0.0	0.0	0.0	0.0	10.0	13.0	0.0	7.6
90	50.0	33.0	0.0	27.6	56.0	40.0	0.0	35.3
85	55.0	43.0	32.6	32.6	60.0	50.0	0.0	36.6
80	56.0	53.0	5.0	38.0	60.0	57.0	11.0	42.6
75	50.0	20.0	0.0	23.3	60.0	26.0	15.0	33.6
70	25.0	24.0	23.0	24.0	28.0	30.0	30.0	29.3

Daldinia concentrica.—The highest temperature of 100° C. for 15 and 10 minutes is obviously harmful to the ascospores of *D. concentrica,* for when treated at this temperature and exposures previous to inoculation, no germination occurred even after

48 hours. Temperatures of 100° C. for 5 minutes and 95° C. for 15 minutes also have a deleterious effect, but the ascospores are not killed, for after 48 hours a very small percentage (1.3 and 1.0 per cent) of them germinated. It is interesting to note that the temperature at which the highest percentage of germination is secured after 24 hours is not the same as that at which the highest percentage of germination is secured after 48 hours. This may be seen at 80° C. for 5 minutes, at which temperature and exposure 38 per cent germination is obtained after 24 hours, while after 48 hours the maximum germination (60 per cent) occurred at 70° C. for 15 minutes. In the range 100° C. for 15 minutes—90° C. for 15 minutes, to which the ascospores were treated previous to inoculation, the swelling was only slight. Thus it appears that too high a temperature will prevent the characteristic swelling of the ascospores which attain an almost square shape, on a medium rich in carbohydrates. This same shape is attained, however, through the range of temperatures and exposures from 85° C. for 15 minutes—70° C. for 5 minutes. Although there are slight variations in the length and width of germ-tubes in the various ranges of temperatures and exposures, the length and width are correlated rather definitely. From 85° C. for 5 minutes through 75° C. for 15 minutes the average measurements are 70–100 × 1.5 μ, while at all of the temperatures and exposures above 85° C. for 5 minutes the tubes are only 25–33 × 3.3 μ. Here the mycelium shows the effects of the higher temperatures by its slow growth and densely granular content. After 24 hours the germ-tubes are not branched; 24 hours later the branching is irregular. A single germ-tube throughout the series is more common than two or an equal number of each, with the exceptions within the range of 80° C. for 10 minutes—75° C. for 5 minutes, where there are equal numbers of ascospores with one and two tubes.

Daldinia vernicosa.—The reaction of the ascospores of *D. vernicosa* to the same treatment received by those of *D. concentrica* is somewhat different. The results of this experiment are given in table III. Only 2 per cent of the ascospores germinated after 48 hours when exposed to a temperature of 100° C. for 10 minutes previous to inoculation. Nevertheless even after such an exposure the percentage of germinated ascospores is greater than that

shown in the controls. The maximum germinations, however, are obtained after the ascospores have been exposed to 75° C. for 10 minutes, when 26.6 per cent produced germ-tubes at the end of 24 hours, and 46.0 per cent after 48 hours when the ascospores were previously subjected to 70° C. for 10 minutes. Thus it becomes quite evident that heat treatment of the ascospores of this species is more stimulating than any previously tried stimuli,

TABLE III

D. VERNICOSA (D. MO.)

PERCENTAGE OF GERMINATION OF ASCOSPORES SHOWING THE EFFECT OF SHORT EXPOSURES TO HIGH TEMPERATURES. EACH EXPOSURE AND PERIOD REPRESENTS A COUNT OF 600 SPORES. PFEFFER AGAR WAS USED

Temp. ° C.	After 24 hrs.				After 48 hrs.			
	Experiments							
	1	2	3	Av.	1	2	3	Av.
	Exposure of 15 minutes							
100	0.0	0.0	0.0	0.0	0.0	1.0	5.0	2.0
95	0.0	8.0	9.0	5.6	13.0	12.0	50.0	25.0
90	0.0	18.0	16.0	11.3	30.0	36.0	25.0	30.3
85	0.0	20.0	20.0	13.3	30.0	32.0	32.0	31.3
80	0.0	55.0	2.0	19.0	0.0	60.0	38.0	32.0
75	6.0	40.0	0.0	15.3	30.0	50.0	43.0	41.0
70	0.0	24.0	7.0	14.0	50.0	51.0	15.0	38.6
	Exposure of 10 minutes							
100	0.0	1.0	1.0	0.6	14.0	6.0	14.0	11.3
95	0.0	9.0	11.0	6.6	46.0	16.0	30.0	30.6
90	4.0	8.0	9.0	7.0	38.0	34.0	26.0	32.6
85	0.0	23.0	22.0	15.0	50.0	39.0	38.0	42.3
80	0.0	54.0	20.0	24.6	36.0	58.0	36.0	43.3*
75	0.0	50.0	30.0	26.6	20.0	58.0	45.0	41.0
70	0.0	50.0	20.0	23.3	41.0	59.0	40.0	46.0
	Exposure of 5 minutes							
100	0.0	2.0	5.0	2.3	9.0	7.0	25.0	13.6
95	0.0	12.0	14.0	8.6	41.0	20.0	24.0	28.3
90	5.0	25.0	17.0	15.6	40.0	44.0	28.0	37.3
85	1.0	13.0	12.0	8.6	40.0	35.0	40.0	38.3
80	2.0	27.0	50.0	26.3	40.0	38.0	60.0	46.0
75	1.0	30.0	5.0	12.0	50.0	44.0	40.0	44.6
70	0.0	20.0	22.0	14.0	40.0	38.0	43.0	40.3

* Conidia after two weeks.

including freezing of the dry ascospores for three months, which treatment only caused 10–15 per cent to germinate. The ascospores never under any circumstances attain the square shape

after swelling, such as is characteristic of the ascospores of *D. concentrica* on a medium rich in carbohydrates, but swelling of the ascospores previously heated at 95° C. for 10 minutes, 90° C. for 15 minutes, 85° C. for 10 minutes, and 80° C. for 5 minutes, is more pronounced than under any previous conditions. Here the ascospores are almost spherical. At higher temperatures, from 100° C. for 15 minutes through 95° C. for 15 minutes, the ascospores are only slightly swollen and at other temperatures and exposures the swelling is considerably more than in the controls where the ascospores were not heated. The germ-tubes also respond in a rather definite manner to the different intensities of heat to which the ascospores are treated previous to inoculation. The germ-tubes which arise from the ascospores exposed to 100° C. for 15 minutes through the intervening temperatures and exposures to 90° C. for 5 minutes are very short and wide, 8–10 × 4.4 μ, while the somewhat longer exposures of the ascospores, 90° C. for 10 minutes through 85° C. for 5 minutes, produced more extensive and narrower germ-tubes, 20–46 × 3.3 μ. The germ-tubes of the ascospores treated at 80° C. for 15 minutes through the intervening temperatures and exposures to 70° C. for 5 minutes grew more rapidly than any of the others; here they were 60–72 × 2.2 μ. In contrast to *D. concentrica* the germ-tubes do branch, one to four times after 24 hours. However, no generalization can be made due to the fact that the branching is too erratic. Branching soon after the germ-tube has grown out from the ascospore is much more common in *D. vernicosa* than in *D. concentrica* under any condition. With one exception, a single germ-tube throughout this series is also more common than two or an even number of one and two. An even number of one and two germ-tubes was produced by the ascospores exposed to 80° C. for 5, 10, and 15 minutes. In comparing the ranges of the two species at which an equal number of one and two germ-tubes occurs, it is seen that they are close together, overlapping at 80° C. for 5 minutes, with *D. concentrica* extending through 75° C. for 5 minutes. Thus it appears that at the temperatures and exposures at which the most rapid growth occurs, in *D. concentrica* at least, an equal number of one and two tubes is found. This does not seem to hold true for *D. vernicosa*, since

the most rapid growth is noted in the germ-tubes from the ascospores which were exposed to 70° C. for 10 and 15 minutes.

A comparison of germination of the two species at the different temperatures and exposures is given graphically in fig. 1. The ascospores of *D. concentrica* do not germinate at the highest temperatures here employed and the high percentages are more uneven in their occurrence than in *D. vernicosa*. For *D. concentrica* 5

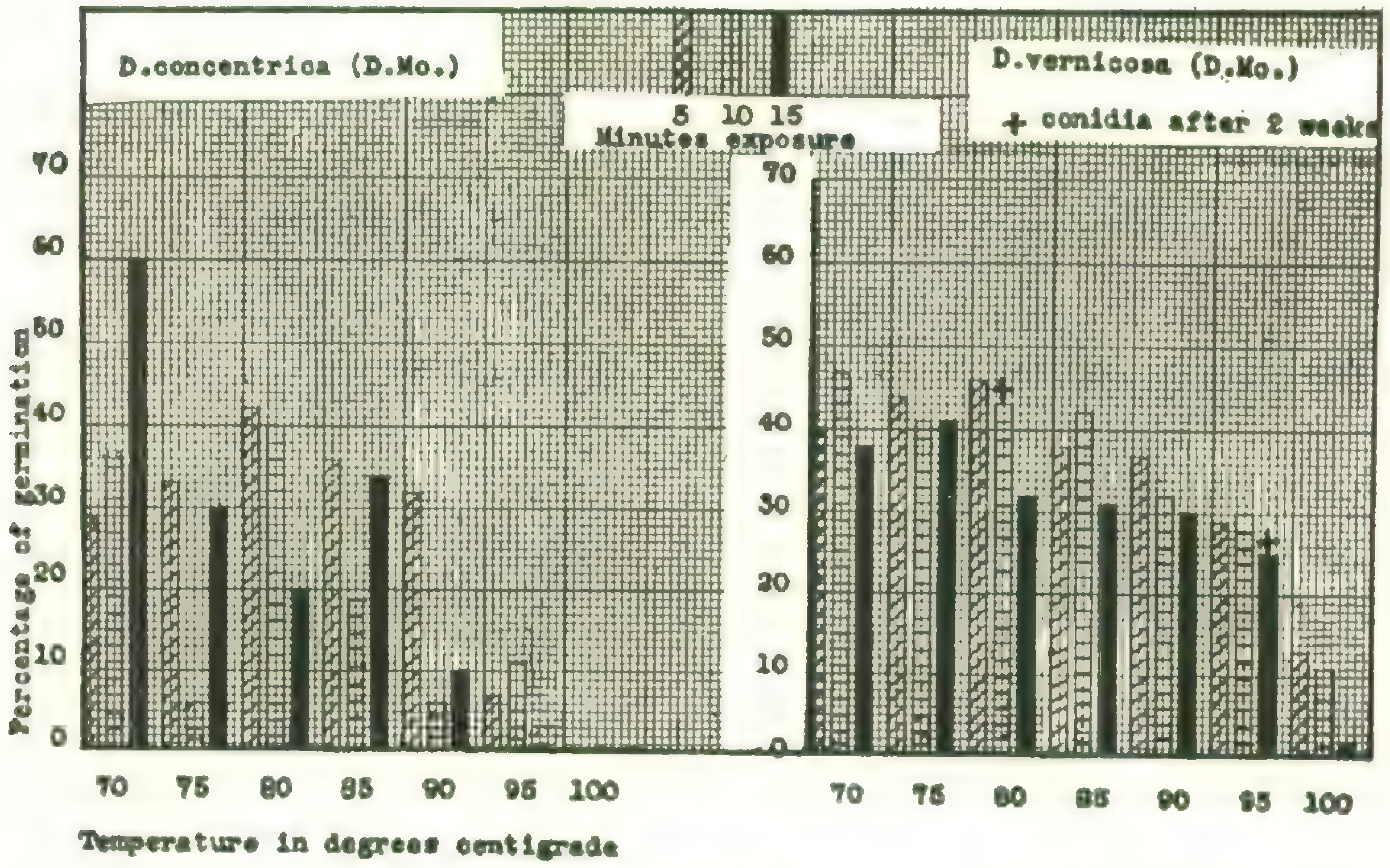


Fig. 1. Ascospore germination showing the effect of short exposures to high temperatures previous to inoculation.

minutes seems to be the optimum exposure, since a more even increase in percentage of germination is indicated, but the maximum percentage is secured at 15 minutes exposure at 70° C. The longest exposure, 15 minutes, appears to be the optimum for *D. vernicosa*, but there are two maxima, one at 80° C. for 5 minutes and the other at 70° C. for 10 minutes; at both exposures 46.6 per cent germination occurred. It is noted in both species that the percentage of germination increases as the temperature and exposure decrease, but even the maximum of 60 per cent germination in *D. concentrica* is not as high as in the controls where 85–90 per cent germination was secured. In both of the species the growth of the germ-tubes is retarded by the exposure to

higher temperatures. This is evident from the fact that the germ-tubes are short and wide with densely granular cell content.

After two weeks the cultures were again examined, this time for conidia. They were found fully developed only in those cultures of ascospores that had been exposed to a temperature of 95° C. for 15 minutes; immature conidia were also found in *D. vernicosa* in those cultures the ascospores of which had been previously treated at 80° C. for 10 minutes, and not at all in *D. concentrica.*

To summarize, it is apparent that short exposures to high temperatures previous to inoculation favorably affect the germination of ascospores of *D. vernicosa.* While the percentage of germination increases as the temperature is lowered from 100° to 70° C. there is a much greater percentage of germination even at 100° C. than in the controls. That an increase in germination occurs when the ascospores are heated is significant when correlated with the fact that *D. vernicosa* usually grows on charred wood. One of the reasons for its rare occurrence is no doubt the fact that its ascospores rarely meet with favorable conditions for germination. Temperature, either high or low, is evidently a very important factor in germination. Whether the inability of the ascospores to germinate is due to the slightly heavier spore wall than that of *D. concentrica* or to a different physiological constitution is difficult to determine. It is a chemical fact that in general an increase in temperature increases chemical activity, and it is also a physical fact that higher temperatures stimulate physical activities which are manifest in swelling. Heat in all of the intensities used probably accelerates chemical activities in the ascospores of *D. vernicosa,* resulting in a higher percentage of germination. The effects of accelerated physical activities are most pronounced in the ascospores treated from 80 to 95° C., at which temperatures the ascospores swelled to a spherical shape. Hence in the case of both species, it seems that short exposures at high temperatures (90° C.) have approximately the same effect as longer exposures at lower temperatures (70–75°C.). At any rate the results of this experiment are illustrative of the fact that there is a decided distinction in the requirements for germination of the two species.

EFFECT OF RELATIVELY HIGH TEMPERATURE IN RELATION TO GROWTH ON VARIOUS MEDIA

The effect of exposing ascospores to high temperatures for short periods of time previous to inoculation has been demonstrated. The object of this experiment is to determine the effect of exposure to relatively high temperatures after inoculation. As a source of nutrition, Leonian, Pfeffer, oatmeal, prune, and *Platanus* decoction agars were used. As a source of heat constant-temperature ovens at 38° C. and at 25° C. were used. *D. concentrica*, five months old, was the only species tested in this experiment. The results are recorded in table IV.

TABLE IV

D. CONCENTRICA (D. MO.)

GERMINATION OF ASCOSPORES SHOWING THE EFFECT OF DIFFERENT MEDIA AND A CHANGE IN TEMPERATURE. THE RESULTS REPRESENT A COUNT OF 800 SPORES ON EACH MEDIUM

Agar medium	Percentage of germination					
	Period of growth					
	24 hrs. at 38° C.			48 hrs at 25° C.		
	Experiments					
	1	2	Average	1	2	Average
Pfeffer	0.0	0.0	0.0	81.0	85.0	83.0
Leonian	11.0	13.0	12.0	29.0	32.0	30.5
Oatmeal	16.0	16.0	16.0	Very good germination; impossible to count percentage because of dense mycelial growth.		
Prune decoction	0.0	0.0	0.0	38.0	32.0	35.0
Platanus decoction	0.0	0.0	0.0	57.0	55.0	56.0

On all of the media after 24 hours at 38° C. it became apparent that the temperature was too high for optimum germination. Those ascospores which had not germinated were apparently plasmolyzed, as indicated by the concavities and large oil globules which had appeared. After counts were made the cultures were put into an oven at 25° C. and counts were again made after 48 hours.

On Leonian agar after 24 hours at 38° C., only 12 per cent of the ascospores had germinated, but all of them were swollen. That the temperature was too high was evident by the low percentage of germination and the germ-tubes which averaged only 18 μ in length and 4.4 μ in diam., and were very granular, and not

branched. After 48 hours at 25° C. there was only 30.5 per cent germination; the other ascospores were plasmolyzed. The germinated ascospores were considerably swollen and the mycelium was short and thick. The ascospores on Pfeffer agar were seriously affected by 38° C., for none of them germinated after 24 hours and they were either only slightly swollen or else plasmolyzed. After the cultures had been put into 25° C., the ascospores recovered from their state of partial plasmolysis, and 83 per cent of them germinated on Pfeffer solution agar. The germinated ascospores swelled to a square shape and the growth of the mycelium, 3.4 μ diam., was characteristically poor. After 24 hours on oatmeal agar the ascospores were considerably swollen, and although 16 per cent germination was secured the mycelium was abundant and 4.4 μ in diam. After transferring to 25° C. the mycelium was so abundant that a count for germination was impossible, although quite obviously the percentage was greater than 50 per cent. Seemingly, because of the high temperature and the high sugar content of the prune-decoction agar, all of the ascospores were plasmolyzed after 24 hours at 38° C., and no germination occurred. After 48 hours at 25° C. 35.5 per cent of the ascospores germinated, were considerably swollen, and the mycelium was heavily granular and much enlarged at the ascospore. The high sugar content of the medium is conducive to short thick and granular mycelium, characteristic of slow growth, the largest attaining an average of 7.2 μ in diameter, while on other media (oatmeal) only 4.4 μ. The ascospores on *Platanus* decoction agar at 38° C. behaved very much the same as those on prune-decoction agar, for after 24 hours none of the ascospores had germinated and were either plasmolyzed or only slightly swollen. On exposure for 48 hours at 25° C., however, the ascospores recovered from their state of partial plasmolysis and 56 per cent germination was obtained. The germinated ascospores had not swollen any further, and the growth of the mycelium was poor, only 3.3 μ diam., and not granular.

From the results of these experiments it is evident that the ascospores will not germinate at as high a temperature as 38° C. after inoculation. This appears to be due to the fact that the ascospores, although able to absorb moisture from the medium,

cannot grow, since heat inactivates the necessary enzymes. The absorption of certain constituents from the medium as a result of the high temperature may also cause in the ascospores a chemical change which is toxic. That the ascospores may recover from a partial state of plasmolysis is shown by changing the cultures to an oven where the atmosphere is 13° C. cooler, since after 48 hours at a temperature of 25° C., the ascospores germinated. Pfeffer agar gives the highest percentage of germination (83 per cent) and *Platanus* decoction agar gives the next best with 65 per cent. While Pfeffer agar is the best medium for ascospore germination, it is the poorest for mycelial growth. Oatmeal agar has proved to be the best medium for mycelial growth and is also probably one of the best media for germination of *D. concentrica* ascospores, although they are so completely enmeshed in mycelium after 72 hours that a spore count is almost impossible.

EFFECT OF DIFFERENT MEDIA

That there is an essential difference between a medium favorable for fungous spore germination and one favorable for growth, Duggar ('01) has noted. He asserts that in general a perfect food is the best stimulus for spore germination of saprophytic forms. From the immediately preceding results it is also noted that there is a difference between a germination medium (Pfeffer agar) and a growth medium (oatmeal agar), but in the case of *D. vernicosa* the stimulus seems to be more important than the food. In studying the germination of a large number of myxomycetous spores, Constantineau ('06) came to the conclusion that carbohydrates alone were insufficient to give good results, although sucrose was a better sugar for germination than glucose. Experiments showed that decoctions of substrata on which the Myxomycetes naturally occurred were favorable for germination. Decoctions of *Platanus* wood, a substratum on which *Daldinia* is found frequently in Missouri, proved to be a favorable medium for germination. The requirements which Maneval ('26) found essential for germination of rust teliospores were oxygen supply, temperature, and maturity, while the substratum and light were of minor importance. This is not true of *Daldinia* ascospores, as is shown by the following tests to determine which of the agar

media used gave the maximum germination at room temperature. The character of the germ-tubes, swelling of the spores, etc. were not regarded here. Material of *D. concentrica*, *D. vernicosa*, and *Daldinia X* was used.

Daldinia concentrica ascospores germinated favorably on all of the media, but Pfeffer solution was the best (80.6 per cent), *Platanus* decoction next (54 per cent), oatmeal third (51.5 per cent), Leonian fourth (47.3 per cent), and prune decoction least favorable with 37.6 per cent germination. According to Wehmer

TABLE V

GERMINATION OF ASCOSPORES SHOWING THE EFFECT OF DIFFERENT MEDIA AT ROOM TEMPERATURE. THE RESULTS REPRESENT A COUNT OF 1200 SPORES FOR EACH SPECIES AND ON EACH MEDIUM

Agar medium	*D. concentrica* (D. Mo.)				*D. vernicosa* (D. Mo.)				*Daldinia X* (V. P. Mo.)			
	Percentage germination after 48 hrs.											
	Experiments											
	1	2	3	Av.	1	2	3	Av.	1	2	3	Av.
Pfeffer	76.0	85.0	81.0	80.6	3.4	4.0	2.5	3.3	1.5	1.0	1.1	1.2
Leonian	47.0	49.0	46.0	47.3	1.0	1.0	1.0	1.0	.7	.4	.7	.6
Oatmeal	54.0	49.0	52.0	51.5	1.1	1.4	1.1	1.2	.6	.5	.7	.6
Prune decoction	35.0	41.0	37.0	37.6	.6	.6	.3	.5	.4	.3	.2	.3
Platanus decoction	54.0	57.0	51.0	54.0	0.0	0.0	0.0	0.0	0.0	0.0	0,.0	0.0

('11), who analyzed the dried fruit of *Prunus domesticus* L., the invert sugar which contains an equal number of glucose and fructose molecules is present in from 23 to 56 per cent and sucrose in 3.9 per cent, but in the dilution of the prune decoction employed in these experiments only approximately 4 per cent sugar is present. Leonian agar, however, is somewhat richer in carbohydrates, for it contains 12.5 per cent maltose and malt extract. From the results with these two agars one would be led to believe that germination is not favored by a medium which contains carbohydrates. However, the results with maltose solutions, as will be shown subsequently, are contradictory to this supposition, for in a 10 per cent solution a high percentage of germination was secured.

The analysis of young twigs and buds of *Platanus occidentalis* have been shown by Wehmer ('11) to vary with the time of year. In analyses made in October, which coincides more nearly to the date of collections by the writer, the following percentages of constituents were given: 44.6 CaO, 7.3 K_2O, 20.0 SO_3, 4.3 P_2O_5, 1.4 Na_2O, 19.0 SiO_2, 1.19 $Fe_2O_3 + Al_2O_3$, 3.4 MgO, 1.7 N, and 10.87 ash. From a decoction of *Platanus* twigs, then, according to this analysis, there are no sugars present. This fact may account for the superiority of *Platanus* decoction over prune decoction and Leonian agars. The reasons for the superiority of Pfeffer agar over Leonian can be deduced, for the composition of these media are more definitely known. Both of these media contain KH_2PO_4 and Mg SO_4, but Pfeffer solution contains 1.00 gram of KH_2PO_4, and 1.00 gram of $MgSO_4$ per liter, while Leonian contains .625 grams of KH_2PO_4 and .625 grams of $MgSO_4$ per liter. Leonian also contains maltose and malt extract as well as peptone which is both a source of carbon (from the lactose present in the meat) and nitrogen (from the proteins), while Pfeffer agar contains no sugars except for the mere trace that may be present in the agar. However, Pfeffer agar contains two sources of nitrogen, in the form of nitrates $Ca(NO_3)_2$ in the proportion of 1.33 grams per liter, and KNO_3 in the proportion of ⅓ gram per liter. From this, it may be deduced that nitrogen must be the constituent which is most valuable in the form of a nitrate. Benecke ('95) considered potassium absolutely necessary for the germination of myxomycetous spores, and when one considers that Pfeffer agar has three different sources amounting to 2.5 grams, while Leonian agar has only one source of 1.25 grams, it seems entirely possible that the potassium as well as the nitrogen source makes Pfeffer's a better medium for germination.

To summarize briefly the results of this experiment, both *D. vernicosa* and *Daldinia X* ascospores germinated better in Pfeffer agar than in any other medium, but the percentages were very low, with only 3.3 per cent of the former and 1.2 per cent of the latter. It is interesting to note that no germination was obtained on *Platanus* decoction agar, which seems to be a perfectly good reason why *D. vernicosa* and *Daldinia X* are not found on *Platanus*. The writer has frequently found *D. concentrica* on *Platanus*

but never the other two species. Leonian and oatmeal agars seemed to be equally good for germination of *Daldinia X*, but oatmeal gave .2 per cent better germination than Leonian for *D. vernicosa.* With the exception of *Platanus* decoction agar, prune-decoction agar for both species appears to be least favorable. If one recalls that a stimulus of heat is necessary for maximum germination of *D. vernicosa,* the low percentages obtained here where no heat was used may be partially explained. As for *Daldinia X*, neither the appropriate stimulus nor medium appears to have been found.

EFFECT OF MALTOSE SOLUTIONS

When sucrose solutions alone were employed as a medium, old ascospores were used, and although considerable swelling was induced no germination occurred. It has been noted that swelling of ascospores is more pronounced on a medium rich in sugars than on one which contains little or no sugar. Since swelling to any extent in general is an indication of likeliness to germinate, a nutrient solution of maltose alone in distilled water was employed. It is known that maltose is a nutritive substance of great value and in living organisms is transferred into assimilable sugar more rapidly than is sucrose. While no particular attempt was made to determine which of the sugars was better for germination, maltose proved to be superior to sucrose. Other investigators have found that sucrose is superior to glucose for germination. Constantineau ('06) found this to be true in an extensive study made on myxomycetous spores. The ability of fungous spores to utilize sugars is so specific that it is a matter of experimentation to determine which disaccharide or which monosaccharide sugar is most available or assimilable.

Three different ranges of maltose solutions were employed in order to secure a fair representation of a most probable range of concentrations favorable for germination. The solutions were sterilized in the autoclave at 15 pounds pressure for half an hour and the usual hanging-drop method of culture adopted. Upon autoclaving the maltose molecule partially breaks down into two glucose molecules, while that of sucrose gives one of glucose and one of levulose. That the two glucose molecules may be more

available as a source of carbon to the ascospores than one of glucose and one of levulose is one factor which probably enters into consideration.

In this experiment ascospores of *D. concentrica*, *D. vernicosa*, and *Daldinia X* one year old and one month old were used, except in the case of *Daldinia X* where the only available material was one month old. The different ages were used in order to

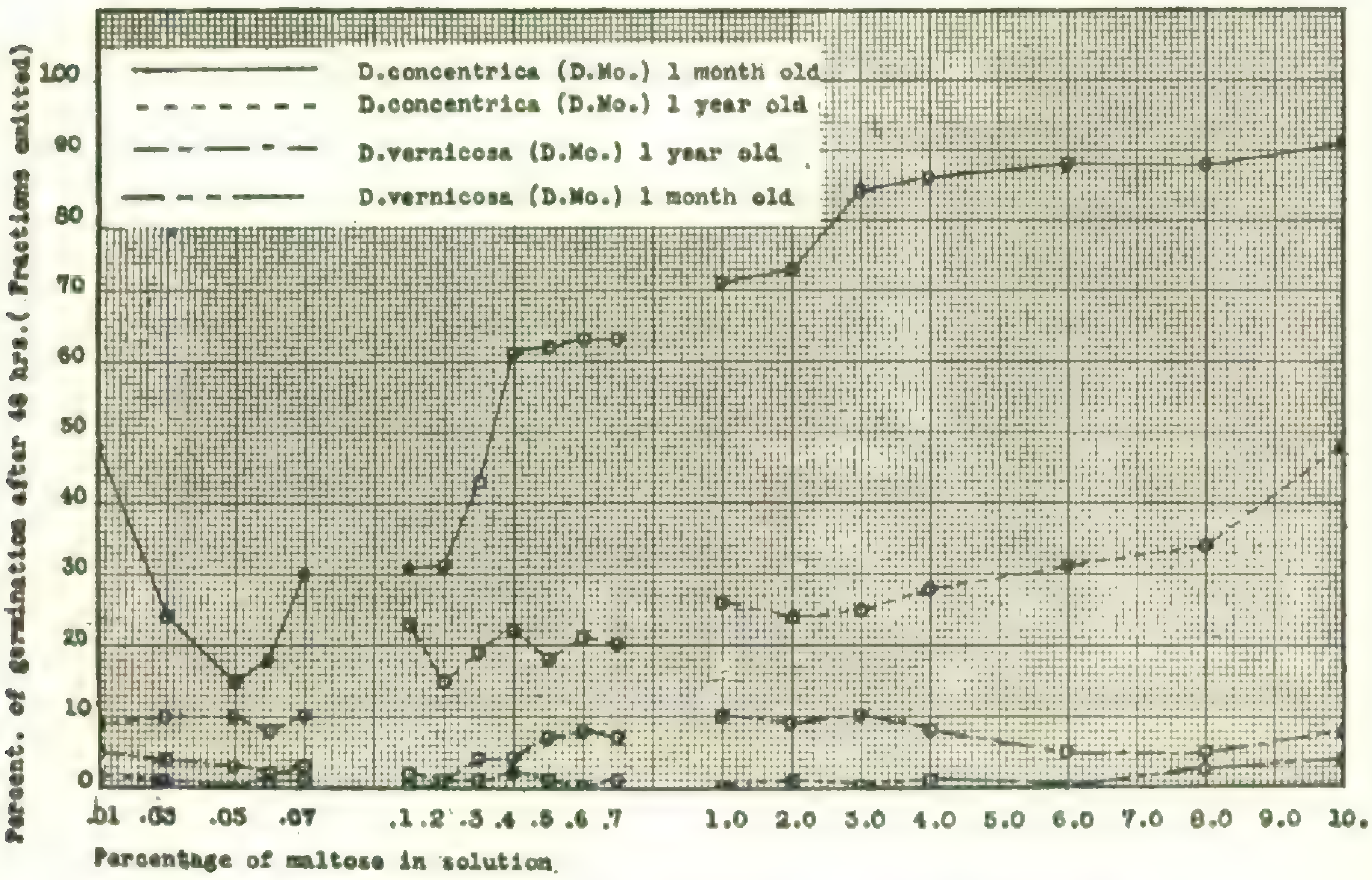


Fig. 2. Germination of ascospores in maltose solutions.

determine whether or not "ripening" or maturation was a factor in germination. The one-year-old material which had been kept in the writer's herbarium had not been fumigated or treated with any disinfectant, nor had the month-old material. The results are given graphically in fig. 2 and in table VI.

Daldinia concentrica.—The percentage of germination in the year-old material from .01 to .07 per cent maltose solutions varied very little, only from 10.6 per cent secured at .03 per cent solution to 8.0 per cent secured at .06 per cent solution. Within this same range the ascospores were considerably swollen, but at higher concentrations from .1 to .7 per cent solutions the swelling was more pronounced. At these concentrations there

TABLE VI

GERMINATION OF ASCOSPORES AFTER 48 HOURS IN MALTOSE SOLUTIONS. IN THE YEAR-OLD MATERIAL, 12,000 ASCOSPORES OF EACH SPECIES WERE COUNTED, WHILE IN THE MONTH-OLD MATERIAL, 8,000 ASCOSPORES WERE COUNTED FOR EACH SPECIES

Percent maltose solution	Percentage of germination													
	D. concentrica (D. Mo.)							*D. vernicosa* (D. Mo.)						
	1 year old				1 month old			1 year old				1 month old		
	Experiments							Experiments						
	1	2	3	Av.	1	2	Av.	1	2	3	Av.	1	2	Av.
.01	10.	5.	12.	9.	46.	50.	48.	11.	3.	3.	5.6	3.	1.	2.
.03	12.	7.	13.	10.6	34.	14.	24.	2.	8.	4.	4.6	1.	0.	.5
.05	10.	10.	10.	10.	15.	16.	15.5	5.	0.	5.	3.3	0.	0.	0.
.06	12.	4.	8.	8.	4.	30.	17.	4.	2.	0.	2.	2.	1.	1.5
.07	20.	6.	5.	10.3	32.	28.	30.	0.	5.	0.	1.6	3.	3.	3.
00.1	15.	10.	46.	23.6	26.	36.	31.0	2.	0.	0.	0.6	2.	2.	2.
00.2	14.	12.	30.	14.6	20.	40.	31.	4.	0.	0.	1.3	0.	2.	1.
00.3	13.	13.	23.	19.6	43.	44.	43.5	2.	8.	4.	4.6	1.	1.	1.
00.4	13.	15.	38.	22.6	64.	58.	61.	3.	9.	0.	4.	1.	3.	2.
00.5	16.	18.	20.	18.	64.	60.	62.	2.	0.	2.	7.3	0.	3.	1.5
00.6	21.	21.	21.	21.	68.	59.	63.5	4.	20.	0.	8.	0.	1.	0.5
00.7	25.	23.	24.	24.	66.	60.	63.	0.	18.	0.	6.	0.	2.	1.
1.00	26.	26.	27.	26.3	68.	74.	71.	10.	22.	0.	10.6	0.	0.	0.
2.00	24.	26.	22.	24.	67.	80.	73.5	3.	25.	0.	9.3	0.	2.	1.
3.00	20.	30.	25.	25.	85.	84.	84.5	5.	27.	0.	10.6	1.	0.	0.5
4.00	16.	30.	40.	28.6	87.	86.	86.5	4.	20.	0.	8.	3.	0.	1.5
6.00	20.	31.	43.	31.3	88.	88.	88.	11.	3.	1.	5.	0.	0.	0.
8.00	25.	33.	44.	34.	90.	87.	88.5	13.	7.	0.	6.6	4.	3.	3.5
10.00	50.	46.	52.	49.	93.	90.	91.5	12.	12.	2.	8.6	3.	5.	4.
Sterile distilled water	16.	17.	16.	16.5	17.	19.	18.	1.	1.	1.	1.	0.	0.	0.

was also a higher percentage of germination, but the percentages were more uneven in their occurrence. At .1 per cent solution there was 23.6 per cent germination, while at .2 per cent solution there was only 14.6 per cent germination, but from .3 to .7 per cent there was an increase again to 24.0 per cent at the concentration of .7 per cent. Germination at 1 per cent solution of maltose reached 26.3 per cent, and from 4 to 10 per cent solution there was a steady increase from 28.6 to the maximum, 49 per cent, germination reached at 10 per cent solution. At these higher concentrations, from 1 to 10 per cent, the ascospores were swollen to a square shape. As to the germ-tubes, a single one was most common throughout the whole series, and most of them were 1.5 μ wide, but the length varied with the concentrations of solutions. From .01 through .4 per cent solutions, the germ-tubes were 175

to 300 × 1.5 to 1.8 μ; from .5 through 4 per cent the tubes were longer, 300 to 500 × 1.5 μ; from concentrations of 6 through 10 per cent there was a variation from 125 to 400 μ. The longest ones (400 μ) in this last series occurred in the 10 per cent solution. The branching of the germ-tubes was more consistently confined to the concentrations from .01 through .03 per cent, while from .05 through .1 per cent they were not branched, as was also true in the solutions from .2 through 10 per cent maltose concentrations.

The month-old material presented an entirely different curve which exceeded the preceding one in height by a difference of 42 per cent germination in the 10 per cent solution. The whole germination curve of the new material was less undulating, except in the lowest concentrations from .01 through .07 per cent. At the former concentration 48 per cent germination occurred, at the latter 30 per cent. The minimum germination in this series was 15.5 per cent, which occurred at .05 per cent solution. The ascospores in this series were only slightly swollen, while in the remaining concentrations the swelling was characteristically square in shape. With an increase in concentrations from .1 through .7 per cent a marked increase from 31 to 63 per cent germination was secured. The germination curve straightened out from 1 through 10 per cent, starting at 71 per cent germination and rising through 73.5, 84.5, 86.5, 88.0, 88.5 per cent, until the maximum percentage of 91.5 per cent was reached. Throughout the series, as in the old material, one germ-tube was most typical, although in the .7 per cent solution, two were more common than one. The two lowest concentrations were least favorable to growth of germ-tubes from ascospores of fresh material, for the tubes averaged 65 × 1.8 μ, and 30 × 1.5 μ. At slightly higher concentrations of solutions from .05 through .7 per cent the average tube ranged from 100 to 30 × 1.5 μ. Within the short range of solutions from 1 through 4 per cent, the germ-tubes were of uniform length and diameter, 500 × 1.5 μ. At the three highest concentrations, growth was less rapid, with only 175 μ in length but the same width. It will be noted that the diameter remains uniform throughout the series except at .01 per cent where there was a difference of .3 per cent.

Thus from a comparison of these results it is seen that the

behavior of the younger material is much more consistent than that of the older. This is true not only of the percentages of germination, but the length and diameter of germ-tubes. Branching of the germ-tubes is under any condition more or less erratic, but the highest concentrations seemed to induce slower growth and no branching, which facts appear to be correlated with the highest percentages of germination. The ascospores are probably able to assimilate the higher percentages to more advantage than the lower percentages. In both cases the higher concentrations of maltose induced more swelling than the lower concentrations. In the controls where sterile distilled water was used the fresher ascospores germinated somewhat better than the older ones. In the former there was 18 per cent germination, while in the latter, 16.5 per cent. The ascospores in both cases were only slightly swollen and the single germ-tubes were not branched. The germ-tubes of the older ascospores were 300 $\times$ 1.5 μ, while those of the younger were only 100 $\times$ 1.5 μ. Evidently the ascospores of *D. concentrica* need no period of rest. "Ripening," or maturation, for maximum germination is secured when comparatively fresh material is used. This is still further proof for the supposition that the ascospores germinate soon after discharge from the perithecia, in the late summer or early fall, and that the fungus lives over the winter period in the vegetative stage. In order to gain more evidence for this hypothesis the effect of freezing the mycelium will be investigated at a later date.

Daldinia vernicosa.—The case of *D. vernicosa* presented almost the opposite picture of *D. concentrica* as seen in fig. 2. From this, it is apparent that in order to secure the optimum germination, a "ripening" or maturation is necessary. Whereas a treatment of artificial wintering by freezing or a heat treatment gave maximum germination, a resting period of a year or so was also effective. The percentages of germination were low when the ascospores were not treated, with a minimum of .6 per cent at .1 per cent solution of maltose and a maximum of 10.6 per cent at 1 and 3 per cent solution. When treated with heat before inoculation as demonstrated previously, 46 per cent germination was secured. In the older material, as a whole, the range of maltose concentrations from 1 through 10 per cent appeared to

be more conducive to germination than the lower concentrations. The lowest concentrations from .01 through .07 per cent induced the least swelling, the second range of concentrations from .1 through 4 per cent induced more pronounced swelling, and the highest concentrations from 4 through 10 per cent stimulated the ascospores to swell to an almost spherical shape. With the exception of from .4 through .7 per cent solution, the ascospores were as light a brown after swelling as they were when treated with H_2O_2. It seems barely possible that the dark brown endospore became oxidized in this case. The maltose solutions at these concentrations may have been less active chemically and thus have prevented a change in color. The number of germ-tubes was very consistent in this group, with an equal number of one and two tubes from .01 through .07 per cent, and in all of the other concentrations one tube was most common. The size of the germ-tube varied considerably. From .01 through .5 per cent solution they were 100 to 195 $\times$ 1.8 to 3.3 μ, and although the diameter of the tubes remained constant, 3.3 μ, from .6 through 4 per cent, the length varied from 300 to 500 μ. The germ-tubes in the three remaining concentrations of maltose solution varied from 100 to 200 $\times$ 1.8 to 2.7 μ. As for the branching of the germ-tubes, the series of concentrations was divided into two parts with little variation; from .01 through .3 per cent the tubes were mostly unbranched and from .4 through 10 per cent they were branched.

The younger material of *D. vernicosa* gave considerably less germination than the older. The maximum percentage of 4.0 per cent was secured in the 10 per cent solution. From the results which are represented graphically in fig. 2, it is seen that the percentage of germination presents an almost straight line. At three concentrations, .03, .6, and 3 per cent, only .5 per cent germination was obtained, while no germination at all was secured at .05, 1, and 6 per cent. Here, as in the older material, definite ranges of concentrations gave different degrees of swelling. At the lower concentrations from .01 through .6 per cent, the ascospores were only slightly swollen, and from .7 through 6 per cent they were considerably swollen. Only at the two highest percentages were the ascospores swollen to a spherical shape.

The range at which an equal number of one and two tubes occurred was almost identical with that of the older material, but one exception occurred at .07 per cent in the younger material where two tubes were more common. The remainder had single tubes. From .01 through .07 per cent solution the germ-tube length and diameter were very consistent with the measurements 200 × 2.8 μ, but from .1 through 6 per cent solution there was a variation from 100 to 200 × 3.3 μ. At the two highest percentages of solutions the narrowest mycelium occurred, and the branches were longer than in any of the preceding concentrations. The germ-tubes averaged 100 × 1.5 μ. Branched germ-tubes were present in all of the concentrations.

In comparing the results of germination of the year-old and the month-old ascospores of *D. vernicosa,* it is evident that the older ones are benefited by their period of "rest." Whereas the percentage of germination in both cases is increased in a 10 per cent solution of maltose, the maximum germination of the older material was not secured at 10 per cent but at 3 per cent and 1 per cent. While the concentrations in which the different degrees of swelling of the ascospores occurred were somewhat different, the degree of swelling was practically the same. The ranges of solutions in which equal numbers of one and two tubes and single tubes occurred were practically the same. In general, the germ-tubes of the older material grew more rapidly than those of the younger, but there was less variation in the length and diameter of the latter than the former. In the younger material where the tubes were not as long as in the older, branching occurred throughout the whole series. In the controls where sterile distilled water was used, none of the new material and only 1 per cent of the older material germinated. In the former the ascospores did not swell at all, but in the latter the swelling was slight and the unbranched germ-tubes averaged 150 × 3.3 μ.

Daldinia X.—Daldinia X, the ascospores of which were about two months old, still further showed a physiological difference by not germinating at all in the maltose solutions. The cultures were kept under observation for six days and, although slight swelling occurred in the lower percentages and more swelling was noted at the four highest percentages, no germination was observed.

Thus a comparison of the results of these experiments still further confirms the differences in the three species and their differences in physiological reactions at different ages.

EFFECT OF DIFFERENT HYDROGEN-ION CONCENTRATIONS ON ASCOSPORE GERMINATION

It has already been seen that the source of nutrition is a factor of great consequence in the germination of ascospores. Maltose, it was found, at a concentration of from 1 to 10 per cent favored germination. Also it has been shown in this paper that Pfeffer solution agar is far more conducive to germination than any of the other media tried. The reasons for this are suggested by Coons ('16), who found that carbohydrates in excess make a medium acid while proteins in excess make it alkaline. With such results it is obvious that hydrogen-ion concentration should be a factor of consequence in ascospore germination.

The toxicity of OH and H ions in this relation has been determined by Clark ('99) for certain mould fungi. He found that certain acids retarded germination and also the early mycelial development. In addition, he demonstrated that the hydroxyl ions were more toxic than the hydrogen ions.

More extensive work concerning the influence of hydrogen-ion concentration on germination of fungous spores was done by Webb ('19, '21), who found that by increasing the concentration in a cultural solution consisting of NaOH, H_3PO_4, and M/5 mannite, the germination of spores of *Fusarium* sp., *Lenzites sepiaria*, *Aspergillus niger*, and other fungi was favorably increased. In further investigations he found that by increasing the acidity of mannite, peptone, and Czapek's solution, sugar beet decoction, "H_2O, H_3PO_4, and NaOH," and "H_2O, HCl, or KOH" from neutrality to approximately pH 3.0–4.0 germination of *Lenzites sepiaria* was stimulated. Beet decoction gave the best range and percentage of germination, while "H_2O, H_3PO_4, and NaOH" gave the poorest. In equal concentrations the OH ions were more toxic than the H ions. The direction and magnitude of the change in the reaction of the medium due to spore germination depend upon the fungus, medium, and initial reaction of the solution. He further says that spore germination is

a process which is strikingly supported by conditions of active acidity; relatively low percentages of germination in most cases are obtained under conditions of active alkalinity. Also the fact is emphasized that the influence of the hydrogen-ion concentration on the germination of spores is dependent upon the nature of nutritive material present in the medium.

Therefore, because of the importance attached to hydrogen-ion concentration it appeared necessary for the sake of completeness to ascertain the influence of hydrogen-ion concentration on the ascospores of *Daldinia*. For this purpose, since material of

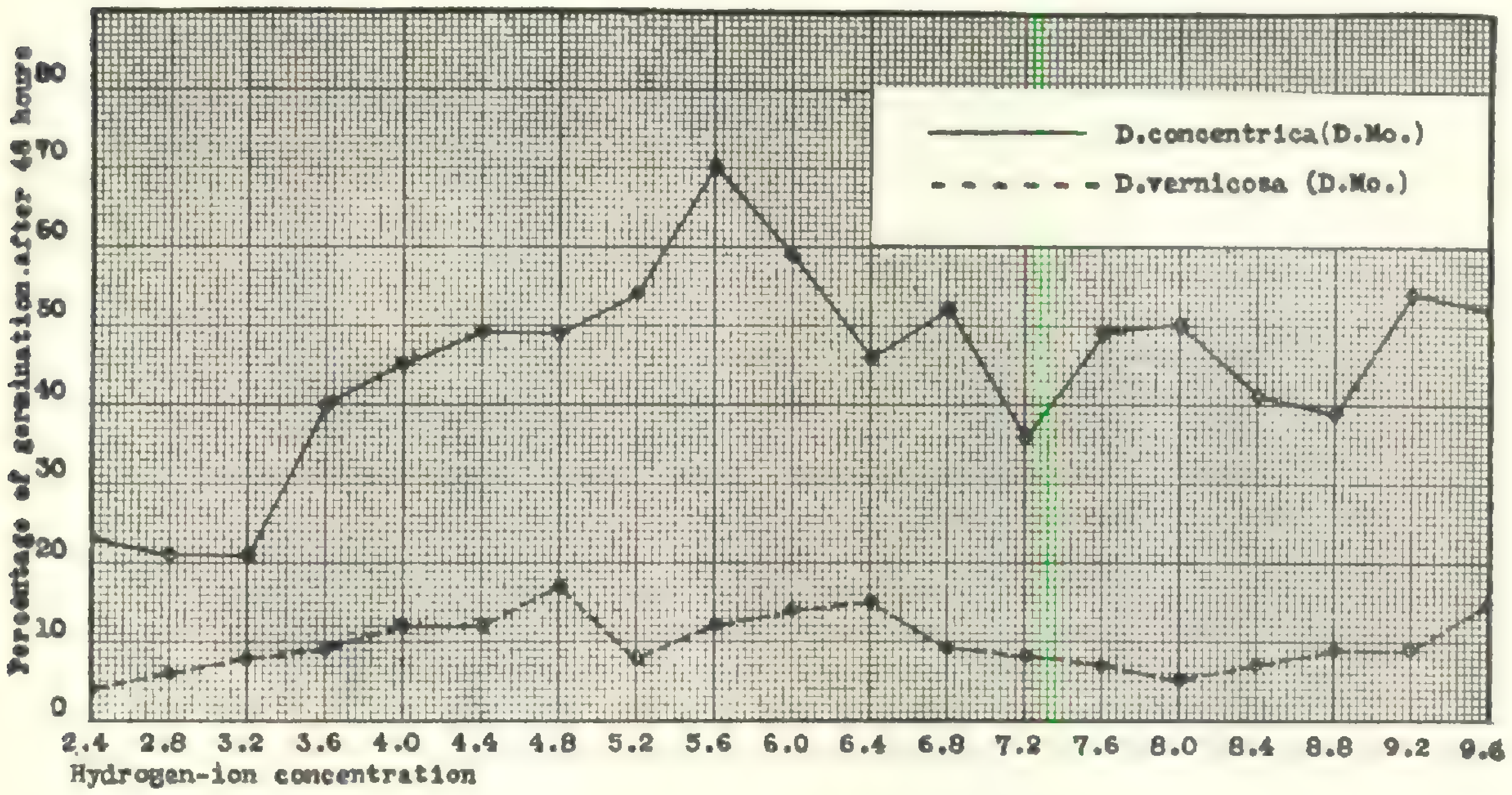


Fig. 3. The effect of different hydrogen-ion concentrations on ascospore germination.

Daldinia X was not available at the time, only the ascospores of *D. concentrica* and *D. vernicosa* were employed; these were five months old. The medium used was Pfeffer's solution made solid by the addition of 3 per cent agar, and adjusted either by citric acid or NaOH. A range of hydrogen-ion concentrations from 2.4 to 9.6 with intervals of .4 was thus obtained. The results given in table VII for *D. concentrica* and in table VIII for *D. vernicosa* are averages of three different experiments representing a count of 22,800 ascospores of each species. Figure 3 represents the percentage of germination of ascospores, but after 48 hours.

Daldinia concentrica.—After 24 hours the percentage of germination rose gradually from 12 per cent at pH 2.4 through 13, 14.3, 19, 22.3, 26.3, 46.3, and 54 per cent, the third highest percentage until the maximum was reached at pH 5.6 where 70 per cent germination was secured. The second highest percentage, 59 per cent, was reached at pH 6.0. At the end of 48 hours these maxima remained the same, no additional ascospores being found to have germinated. At the extreme alkaline end of the series (pH 9.6) 35.0 per cent germination was secured. As is shown by fig. 3, which represents the percentage of germination after 48 hours, there was an increase over that obtained after 24 hours. Nevertheless the range in which the highest percentages were secured remained within the narrow limits from pH 5.2 to 6.0.

The character of the ascospores and germ-tubes was noted only after the 24-hour period. At this time throughout the whole series of hydrogen-ion concentrations, the ascospores swelled to an almost square shape with the exception of a narrow range on either side of neutral. This range included the hydrogen-ion concentrations from pH 5.6 through 7.6, in which all of the ascospores were swollen but only the germinated ones had attained the characteristic square shape. Thus it appears that extreme acidity or alkalinity will induce swelling of the ascospores, whether they germinate or not.

Throughout most of the series the ascospores produced either one or two germ-tubes, the number of which were about equally divided. At pH 6.0, 6.4, and 8.8, however, the ascospores most commonly produced two germ-tubes, a fact which is indicative of a fair degree of correlation with the optimum of germination. At the same time the growth of germ-tubes was most rapid at pH 7.6 at which point the average size was 325 × 4.4 μ. On the other hand, growth was least rapid at pH 4.0, only 39 × 3.3 μ. At the remaining concentrations the germ-tubes were mostly 100 × 3.3–4.4 μ. Between the hydrogen-ion concentrations of 2.4–4.4 and 8.0–9.2 the diameter of the germ-tubes was quite constantly 3.3 μ, while from 9.2 to 9.6 they were 2.2 μ. Branching occurred at all concentrations except pH 2.4, 4.0, 6.8, and 7.2; each tube had from one to four branches and in most cases the branching was correlated with rapid growth; this was especially true at pH 5.6 and 7.6.

TABLE VII

D. CONCENTRICA (D. MO.)

GERMINATION OF ASCOSPORES AT DIFFERENT HYDROGEN-ION CONCENTRATIONS. THE RESULTS REPRESENT A COUNT OF 1200 ASCOSPORES FOR EACH HYDROGEN-ION CONCENTRATION, WITH PFEFFER AGAR AS THE MEDIUM

pH	Percent germination after 24 hours				Character of germ-tube. Length in microns	Branching —No. per spore	Conidia produced after days		
	Experiment								
	1	2	3	Av.			16	24	29
2.4	10.0	4.0	22.0	12.0	58.5c	0	+		
2.8	12.0	13.0	14.0	13.0	53.5c	1–4	−	−	+
3.2	12.0	14.0	17.0	14.3	55.0a	1–2	−	−	−
3.6	18.0	20.0	19.0	19.0	191.6c	1–2	−	−	−
4.0	20.0	23.0	24.0	22.3	39.0a	0	−	−	−
4.4	21.0	32.0	25.0	26.3	260.0a	2–3	−	−	−
4.8	44.0	46.0	49.0	46.3	206.0a	2–3	+		
5.2	64.0	32.0	66.0	54.0	170.0c	2–4	+		
5.6	73.0	74.0	63.0	70.0	251.3c	1–2	+		
6.0	52.0	69.0	56.0	59.0	126.6b	1–2	−	−	−
6.4	41.0	59.0	35.0	45.0	224.0b	3–4	−	−	+
6.8	53.0	40.0	63.0	52.0	41.0c	0	+		
7.2	41.0	31.0	33.0	35.0	77.3a	0	−	−	−
7.6	47.0	38.0	50.0	45.0	325.0c	1–4	−	−	+
8.0	40.0	31.0	43.0	38.0	94.0a	1–2	−	−	−
8.4	31.0	29.0	30.0	30.0	60.1a	1–3	−	−	−
8.8	30.0	27.0	45.0	34.0	83.0b	2–3	−	−	−
9.2	45.0	51.0	51.0	49.0	74.0c	1–2	−	−	+
9.6	27.0	35.0	43.0	35.0	180.0a	1–2	−	+	

a = majority with one germ-tube.
b = majority with two germ-tubes.
c = equal number with one and two germ-tubes.
\+ = conidia present.
− = conidia absent.

The cultures were examined for conidia at three periods, at the end of 16, 24, and 29 days. After these periods the mycelium had so completely grown over the cover-glasses that it was impossible to see conidia without resorting to the use of a stain, for which purpose cotton-blue in lacto-phenol was employed. The conidia, which take the blue stain, are then easily seen. For each hydrogen-ion concentration four preparations were made at each period in order to eliminate as far as possible any experimental error. In the most acid concentrations of pH 2.4 conidia were present after 16 days. After this same length of time conidia were present in cultures started at pH 4.8., 5.2, 5.6, and 6.8. At all other hydrogen-ion concentrations no conidia were

observed. When 24 and 29 days had elapsed conidia were found also at pH 9.6, and at 2.8, 6.4, 7.6, and 9.2 respectively. Thus it appears that within a certain acid range and within a certain alkaline range conidia will not develop. Of course the absence of conidia may have been due to some other factor than hydrogen-ion concentration. In a hanging-drop culture in which the medium is present in such small quantities the food supply might soon be exhausted by the mycelium rapidly covering the medium. In most cases the cultures did not dry out, due to the maximum amount of solution placed in the cell when it was made up and due to the thorough sealing by vaseline. Therefore, although food supply is a very important factor in the occurrence of conidia, hydrogen-ion concentration also plays a very important role in the production of conidia.

Daldinia vernicosa.—With the identical treatment received by the ascospores of *D. concentrica*, the ascospores of *D. vernicosa* after 24 hours gave a characteristically poor percentage of germination. The maximum germination of 3.5 per cent was reached at pH 6.4. At pH 4.0, 4.4, and 4.8 there was 3 per cent germination, and 2.5 per cent, the next highest, occurred at pH 6.0. At pH 6.8, 2 per cent germination, and at pH 7.6 and 8.8 only 1 per cent germination was obtained. Only .5 per cent more was secured at pH 9.2. At the remaining hydrogen-ion concentrations there was no germination.

After 48 hours the percentages increased in every hydrogen-ion concentration, with a maximum of 17 per cent at pH 4.8 and a minimum of 4 per cent at pH 2.4. At the extreme alkaline end of the series the ascospores were stimulated, since 15 per cent germination occurred. The same percentage occurred at pH 6.4. The hydrogen-ion range as seen in fig. 3, from 4.0 through 6.4, was definitely the most favorable for germination, although the extreme alkaline medium of pH 9.6 stimulated the ascospores to nearly maximum germination.

The ascospores at the two extremes, pH 2.4 through 3.6, and pH 8.0 through 9.6, after 24 hours were only very slightly swollen, even though germination did occur at 8.8 and 9.2. In the intervening hydrogen-ion concentrations the swelling was slightly more pronounced, but at no hydrogen-ion concentration did the

swelling approximate that of the ascospores subjected to heat previous to inoculation. One germ-tube was the most common, although two did occur in some cases. The diameter remained constant, 4.4 μ, throughout the series, but the length varied; the longest germ-tubes occurred at pH 4.4 where the average length was 33 μ; the shortest one, 15.5 μ, occurred at pH 6.0. Most of the germ-tubes were not branched after 24 hours, but

TABLE VIII

D. VERNICOSA (D. MO.)

GERMINATION OF ASCOSPORES AT DIFFERENT HYDROGEN-ION CONCENTRATIONS. THE RESULTS REPRESENT A COUNT OF 1200 SPORES FOR EACH HYDROGEN-ION CONCENTRATION, WITH PFEFFER AGAR AS THE MEDIUM

pH	Percent germination after 24 hours. Experiment				Character of germ-tube. Length in μ	Branching —No. per spore	Conidia produced after days		
	1	2	3	Av.			16	24	29
2.4	0.0	0.0	0.0	0.0	0	0	−	−	+
2.8	0.0	0.0	0.0	0.0	0	0	−	−	−
3.2	0.0	0.0	0.0	0.0	0	0.	−	−	−
3.6	0.0	0.0	0.0	0.0	0	0	−	−	+
4.0	4.0	2.0	3.0	3.0	22.0a	0.	−	−	−
4.4	3.0	3.0	3.0	3.0	33.0a	1–2	−	−	−
4.8	5.0	3.0	1.0	3.0	30.0a	2–4	−	−	−
5.2	0.0	0.0	0.0	0.0	0	0	−	+	
5.6	0.0	0.0	0.0	0.0	0	0	−	−	−
6.0	2.5	3.0	2.0	2.5	15.5a	0	−	−	−
6.4	4.0	3.5	3.0	3.5	17.0a	0	−	−	−
6.8	2.0	2.0	2.0	2.0	27.0a	0	−	−	−
7.2	0.0	0.0	0.0	0.0	0	0	−	+	
7.6	1.0	1.0	1.0	1.0	19.5a	0	−	−	+
8.0	0.0	0.0	0.0	0.0	0	0	−	−	−
8.4	0.0	0.0	0.0	0.0	0	0	−	−	−
8.8	2.0	0.0	1.0	1.0	22.0a	0	−	+	
9.2	3.0	1.5	0.0	1.5	24.0a	0	−	−	−
9.6	0.0	0.0	0.0	0.0	0	0	−	−	−

a = majority with one germ-tube.
\+ = conidia present.
− = no conidia.

at pH 4.4 and 4.8 where the longest tubes occurred, one to four short branches were noted. After 16 days no conidia were observed; after 24 days conidia were found in cultures of pH 5.2, 7.2, and 8.8; and after 29 days conidia were found at pH 2.4, 3.6, and 7.6.

It is clear from the above experiments that the hydrogen-ion

concentration of the medium is a factor in the germination of the ascospores of *Daldinia concentrica* and *D. vernicosa;* both of these species find most favorable conditions between pH 4.8 and 6.0, although the latter species was greatly stimulated at pH 9.6. Extreme acidity and alkalinity with the exception noted were not conducive to germination. In general this conclusion can be said to agree with Panisset ('29), although unfortunately it is impossible to correlate her results with those of the writer's, since Panisset's are not stated quantitatively. Furthermore, she has adopted an arbitrary method of expressing acidity and alkalinity and her medium was a sucrose solution without the addition of mineral salts. As she demonstrated, and the writer has observed, differences of the substratum give different results in germination. Yet in spite of the differences of method it is clear that the ascospores tolerate a wide range of acid and basic conditions.

FACTORS INFLUENCING THE GROWTH OF MYCELIUM

THE EFFECT OF LIGHT AND DARKNESS

The effect of light and darkness on fungi is usually studied in reference to the production of fruiting bodies, and a great deal of work has been done on some of the well-known groups of fungi, such as *Saprolegnia*, *Mucor*, *Pilobolus*, etc. As seen by Lendner ('96), spores of *Mucor flavidus* were produced only in light; *Mucor racemosus* developed sporangia in darkness but the spores reached maturity only in light. Many species of moulds were found to show an excessive elongation of the sporophores in darkness.

The influence of light upon vegetative and reproductive processes of several algae and fungi was noted by Klebs ('96), who observed that the appearance of zoospores occurred most frequently in diffuse light and darkness, but conjugation took place in light. The intensity and duration of the illumination were the factors in the influence. The blue-violet rays appeared to be the cause of the specific action of light in such instances. A few years later Klebs ('00) asserted that light exerted no influence; growth of the vegetative, as well as the reproductive, organs of many fungous forms was utterly uninfluenced by the radiation. The growth of the sporophores in many species occurred absolutely regardless of light and darkness. Transpiration and nutrition may mask or alter the effects of illumination.

The observations of Stameroff ('97) offer some important and accurate evidence upon the influence of light upon the growth of fungi. Vegetative hyphae of *Mucor* and *Saprolegnia* show the same rate of growth in light and in darkness, while light is found to retard the elongation of the sporangiophore of *Mucor*.

Bullot's ('97) observations demonstrated that the growth of the sporangiophores of *Phycomyces* and *Mucor* was accelerated by diffuse light, thus substantiating the results of previous workers. It has been demonstrated by Grantz ('98) that *Pilobolus* formed sterile sporangiophores in darkness, but the etiolated sporangiophores might produce spores if given only 15 minutes exposure to light. He suggested that the etiolation phenomena of fungi are in fact reactions to the specific stimulations of light and darkness, and that various correlations are exhibited in these reactions.

In ascertaining the factors which determine the formation of pycnidia in *Plenodomus fuscomaculans*, Coons ('16) claims that, regardless of the media used, light is necessary for the formation of pycnidia. The process of the fruiting body formation is one which depends upon the metabolism of the fungus, and the direct result of the presence of light is oxidation, which may be brought about more rapidly by a higher temperature or richer food, in turn bringing about a more rapid metabolism. Thus the increased reproduction would be traced to the effect of oxidation. To confirm this, Leonian ('24) has shown the value of the presence of light as an oxidizing agent in the formation of pycnidia in some of the *Sphaeropsidales*. Occasionally a higher temperature not only replaced the effect of light, but became a more efficient agent for the promotion of fruiting. This was shown by subjecting cultures to light and darkness at room temperatures, then darkness at a constant temperature of 30° C. and light for 24 hours, then dark for 24 hours at 8° C. The effect of light may be traced to some series of photochemical changes which result in the inception of reproductive bodies. The aerial-branch systems have the potentiality of developing into reproductive structures before they receive energy from light. This is explanatory of degenerative structures which arise in darkness in equivalent positions to apothecia in normal cultures. The

relation of light to reproductive activity in this fungus thus operates relatively late upon regions of mycelium where the potentiality for development in a definite direction has already been determined. The absorption of a certain amount of energy from light is therefore a final phase in the sequence of causation concerned in the development. There are other factors which are concerned in this problem but one of the important ones is the presence of enzymes. Blackening observed in the absence of light in this case is said to be due to the abnormal effects of oxidizing enzymes, but light will inhibit these abnormal effects.

In the writer's experiment, the influence of light and darkness was regarded in relation to growth of the mycelium and not to the production of fruiting bodies, as the factors concerned in the formation of the perfect stage of *Daldinia* will be treated in a later paper. Since darkness proved to be more favorable to the germination of ascospores, its influence checked against that of light was tried here.

The source of inocula was mycelium from single ascospore cultures of *D. concentrica* (D. Mo.) (5 months old) and from mycelium developed from small bits of stromatic material in the case of *Daldinia Y* (B. S. D.) and *D. vernicosa* (C. Mass.), all of which were grown on oatmeal agar. Approximately one square centimeter of actively growing mycelium of the same age in each species served as the inocula. Four Erlenmeyer flasks of 250-cc. capacity with about 100 cc. of oatmeal or Pfeffer agar were made up for each species. Two were placed in the light of a north window at room temperature and two were put into a thoroughly darkened cabinet which was approximately at room temperature. The cultures were examined after 5, 10, 12, and 30 days.

Daldinia concentrica.—On oatmeal agar the cultures in the dark developed a much more aerial, denser, and more abundant mycelium than the ones in the light. The mycelium grew about twice as rapidly in the former as in the latter. The tufts of mycelium in both cases were small, at first white, but after 30 days the one in the light was noted to have changed to a "Pallid Mauve Gray,"[1] then to a "Mouse Gray" in the lightest portions,

[1] Ridgway, R. Color standards and color nomenclature. Washington, D. C. 1912, used where colors are in quotation marks.

and finally to a "Quaker Drab" in the darkest portions. Where coming in contact with the glass the mycelium became blackened. In the dark the mycelium underwent changes of color, but in a very much milder degree. No blackening was noted, and it was therefore supposed that continuous light was necessary. The short exposures to light when the cultures were examined seemed to be sufficient stimulation to cause changes from white to "Pallid Mauve Gray." Later, cultures of *D. concentrica* were put into the dark and not examined for 30 days, after which time the mycelium had changed very little from white to a "Pale Dull Gray." The medium did not change appreciably in color, except for the slight darkening due to the blackened mycelium in contact with the glass.

Zonation was observed in the cultures kept in the light and darkness, but it was more pronounced in the former. Conidia in the cultures of this species, as well as of *D. vernicosa,* as far as the writer has observed, are usually associated with the presence of zones. The zones are apparently correlated with the rate of growth, for in the light, where the mycelium grows less rapidly than in the darkness, the zones are more distinct. It would seem then that the zones are formed as the result of staling products, and the check in growth induces the formation of conidia on a favorable medium.

On Pfeffer agar the mycelium responded in a similar way to light and darkness. The only difference was noted in the characteristic delicacy and sparseness of growth, due to the lack of carbohydrates in the medium.

Daldinia Y.—Under the same conditions as *D. concentrica* the mycelium of this species grew less rapidly at first, but after ten days the growth proceeded rapidly and at the end of the experiment far exceeded the quantity and extent of mycelium of *D. concentrica.* After 5 days the radial growth of the mycelium in the dark was about .7 cm., was dense and cottony, while in the light the growth was .5 cm., and was more delicate and appressed. After 10 days the mycelium in the dark had a radial growth of about 6.5 cm. and was very dense and cottony, while in the light the radial growth was only about .5 cm. less, but the mycelium was prostrate and began to take on a cottony appearance due to

its increasing abundance. The mycelium of cultures kept in the dark had covered the surface of the agar after 12 days, and a ring of 11 small turbinate tufts of mycelium and one tuft at the place of inoculation gave the culture a very nodular appearance. In cultures exposed to light the mycelium had also covered the surface of the medium, and two large fused turbinate tufts of mycelium were noted at the place of inoculation, while several smaller less distinct tufts were scattered over the surface of the medium. After 30 days the cultures in the dark had developed further and the large turbinate tufts of mycelium strongly resembled ascocarps (pl. 36, fig. 2). The mycelium had grown up on the sides of the flask and under the medium and had become a "Light Buff" color. In the light the mycelium was a "Vinaceous Buff" color; it had grown less rapidly than in the dark and had not grown up on the sides of the flask or under the medium. A secretion, dilute "Claret Brown," oozed out from the medium and collected in small droplets over the surface of the mycelium in cultures maintained in the dark and only after two months of growth.

A similar series of experiments on the effect of light and darkness, with Pfeffer agar as the medium, was carried out. Here again this medium proved to be a poor one for mycelial development, but the different effects of light and darkness on the growth were equally evident. In both cases the mycelium was delicate, although in the dark it was slightly denser, more aerial, and grew about one and one-half times more rapidly than in cultures exposed to light. Zonation was more definite in the light than in the dark.

Daldinia vernicosa (C. Mass.).—With the same treatment as the two preceding species, the mycelium of *D. vernicosa* on oatmeal agar grew very luxuriantly; darkness was more conducive to rapid and dense growth of mycelium than light. In the dark the mycelium was densely cottony, while in the light it was more delicate, sparse and uneven, at first white, then after 30 days a "Pale Pinkish Buff," and the medium had turned a "Hazel" color. A dilute "Claret Brown" secretion oozed out from the medium and collected in small droplets over the surface of the mycelium which by this time had become leathery. The secretion

was also noted in the culture in the dark but in the light there was a greater quantity.

On Pfeffer agar, the mycelium responded in a similar manner to that on oatmeal agar when exposed to light and darkness, except the growth was less abundant and more delicate.

Although this experiment was undertaken primarily with further work in mind to determine under what conditions of light the mycelium grew more favorably, results have been so illustrative that they are considered a part of this study. Thus the results are in agreement with those of the investigators who have found that the mycelium of certain fungi grow more rapidly in the dark than in the light. Light does retard growth, as some workers have demonstrated with other fungi. No doubt the medium plays a part in the growth response, as is seen in the cultures where Pfeffer agar was used, but the cultures in the light and dark were distinct on both oatmeal and Pfeffer agars in all three species. In general, the mycelium in the dark grew more rapidly, more upright and more evenly than in the light. The great abundance of growth in both light and darkness was characteristic of *Daldinia Y*. The heavier growth of mycelium was probably not the result of the use of stromatic material, since even from single ascospore cultures of *D. vernicosa* the mycelium was almost as abundant as in the case of *Daldinia Y* derived from stromatic material. Still further proof of this contention is found in sprayed ascospore cultures of *D. concentrica* which were allowed to develop mycelium from hundreds of ascospores, and the volume of growth never attained that of *Daldinia Y*. Next to *Daldinia Y*, *Daldinia vernicosa* developed the most abundant mycelium, whether from a single ascospore or from a bit of stromatic material. Although the ascocarp of *Daldinia Y* and *D. concentrica* closely resemble one another, in behavior and appearance the former species in culture more closely resembles *D. vernicosa*.

The "Claret Brown" secretion of *D. vernicosa*, it will be remembered, developed in cultures exposed both to light and to darkness after a month, but in the case of *Daldinia Y*, only after 2 months in the dark. The secretions were not observed in the cultures where Pfeffer agar was used. It might be deduced that the secretion develops only on a medium rich in nutrient materials.

That this may very likely be true is suggested by the fact that *Avena sativa* grain (according to Wehmer) contains about 50–60 per cent starch and 2–5 per cent sucrose and dextrin. On the other hand, the secretion may be associated with the staling of the culture and may be a metabolic product of the fungus formed as a result of age or moisture. It has been stated that the direct result of the presence of light may be oxidation, and the photochemical changes might account for the presence of the secretion, were it not for the fact that the secretion appears in the dark as well as in the light.

The blackening of the mycelium of *D. concentrica* in contact with the glass was observed in month-old cultures in the light, but not in the dark. Very little color change of the mycelium occurred when the cultures were in continuous darkness, although in a parallel series very short exposures (not exceeding five minutes) at several intervals resulted in distinct changes. Thus it appears that the blackening is due to an oxidation process which is probably stimulated by light. Blackening never occurs in *Daldinia Y* or in *D. vernicosa*.

Conidia were produced by all three species irrespective of whether the cultures were maintained in darkness or light, yet in the light they were more abundant, especially in the denser parts of the zone.

THE EFFECT OF DIFFERENT MEDIA AND DIFFERENT TEMPERATURES

The nutrition of the fungi has for years been a subject demanding the attention of many investigators, but parasitic forms have engaged interest more than saprophytic forms, because of their economic importance. The sources of carbon and nitrogen have been varied in all sorts of media formulae and in most cases have proved to be entirely specific in their requirements. Webb ('21) found that the fungi which he used did not grow as well in a medium where cellulose was a source of carbon as where the sugars and peptones were a source. Organic forms of nitrogen were superior to inorganic forms. Wolpert ('24) states that monobasic salts are better for fungous growth, while di- and tribasic salts, since they are alkaline, inhibit the growth of mycelium. Brown ('23), who studied six strains of *Fusarium*, found that by

increasing the glucose in the medium, more aerial mycelium developed, and with an increase in the phosphate form of neutral salts and in starch, sporulation was stimulated while aerial mycelium was inhibited. With an acid phosphate the results were the opposite. Color in the medium was found to be due to a high carbon and nitrogen ratio together with a low phosphate concentration.

Another important factor in the development of fungi is temperature. The combined effect of substratum and temperature is in all probability a factor in mycelium development of many fungi which cannot be neglected. The following experiment shows that this is true for members of this genus.

As a source of heat, constant-temperature ovens of 23–24° C., 27–28° C., and 32–33° C. were employed. Triplicate cultures were made in petri dishes with *Platanus* decoction, Leonian, Pfeffer, and oatmeal agars as the media. The experiment was performed two different times, and an average of these was calculated. The plates were inoculated in the usual manner with mycelium developed from single-spore cultures of *D. concentrica* (D. Mo.) and *D. vernicosa* (D. Mo.) (both five months old), but the mycelium of *Daldinia Y* (B. S. D.) was developed from small bits of stromatic material. Readings were taken after 48, 120, 168, and 216 hours, then the rate of growth per day was calculated at 120 hours in the case of *D. concentrica* and *Daldinia Y*, and at 48 hours in the case of both *D. vernicosa*, since by these two periods the mycelium had almost covered the surface of the medium. The results are given in tables IX, X, XI, and XII.

Daldinia concentrica.—On *Platanus* decoction agar most rapid growth, 15.66 mm. per day, occurred at 27° C.; slightly less rapid growth, 12.33 mm. per day, at 23° C.; while the least occurred at 32° C., with 11.00 mm. per day. At all temperatures the growth was even but delicate, although at 23° C. the mycelium was at first aerial but became prostrate at the end of 48 hours. At the two higher temperatures the colonies were prostrate from the beginning.

The most rapid rate of growth per day, 12.33 mm., on Leonian agar, was obtained at 23° C. Here 27° C. was second best with 11.66 mm. growth per day, and the growth seemed to be rather

slow at 32° C., with only 5.33 mm. per day. On this medium at all temperatures the mycelium was aerial, and the growth was even, fine, but dense. At all temperatures one zone appeared after 120 hours, but at 32° C. an additional zone appeared by the end of 168 hours. Zones in these cases indicated the presence of conidia, which were present in all cultures at 120 hours.

On Pfeffer agar the mycelium grew fairly rapidly, but it was extremely delicate. The most rapid rate of growth per day, 13.33 mm., was secured at 27° C.; at 23° C. the next highest of 10.00 mm. occurred; while at 32° C. the mycelium was least extensive or 7.66 mm. per day. The mycelium on this medium at 23° C. was characteristically appressed after 48 hours, although until 24 hours it had been aerial. At higher temperatures it was at first prostrate, but then became appressed. The growth of mycelium at 23° C. and 27° C. was uneven, although at 32° C. it was even. Delicate, fuzzy mycelium was not confined to any one temperature. Conidia were produced only at 32° C. after 124 hours.

TABLE IX

D. CONCENTRICA (D. MO.)

THE EFFECT OF DIFFERENT MEDIA AND DIFFERENT TEMPERATURES ON RADIAL GROWTH OF MYCELIUM

Medium	Temp. °C.	Mm. growth after hours				Rate of growth per day at 120 hrs. in mm.
		48	120	168	216	
Platanus decoction agar	23 27 32	20 22 18	57 69 51	PC PC 72	PC PC PC	12.33 15.66 11.00
Leonian agar	23 27 32	20 15 14	57* 50* 30*	PC PC 50	PC PC PC	12.33 11.66 5.33
Pfeffer agar	23 27 32	8 14 24	38 54 47*	52 PC PC	PC PC PC	10.00 13.33 7.66
Oatmeal agar	23 27 32	16 11 12	48 27* 23*	61 47 28	PC 60 34	10.66 5.33 3.66

PC = plate covered
* = conidia present.

Oatmeal agar, which has usually proved to be the best medium for mycelial growth, here actually proved to be a medium on

which the mycelium grew more slowly than any of the other media tried. Although the rate of growth was slow, more luxuriant and dense mycelium was produced. The greatest rate of growth per day, 10.66 mm., was secured at the temperature nearest that of room temperature, 23° C.; at 27° C. growth was 5.33 mm., and at 32° C. was only 3.66 mm. per day. On this medium, as was characteristic under all conditions tried, the mycelium was aerial. After only 24 hours, the growth of the mycelium was even, very dense and fluffy, while after 120 hours the nodular character of the mycelium had become evident, and at all temperatures there were no zones present, but at 27° and at 32° C. conidia were observed.

Daldinia Y.—The three temperatures seemed to be almost equally favorable for the growth of the mycelium of *Daldinia Y* on *Platanus* decoction agar. There was a slightly better growth at 23° C. than at the other temperatures, but the rate of growth was rapid, 10.33 mm. per day. This medium which has proved to be a rather poor one for profuse development of mycelium, was not conducive to aerial mycelium. At 23° C. and 27° C. the growth was even, but at 32° C. it was uneven, and at all three temperatures the mycelium was prostrate, very delicate, azonate, and no conidia were present.

On Leonian agar the rate of growth was rapid, for at 27° C. the surface of the agar was covered after 120 hours, and 32° C. was favorable as shown by the 13.33 mm. of growth per day. Only 7.33 mm. growth per day was obtained at 23° C. At the highest temperature the mycelium was prostrate after 24 hours, then slightly aerial, but at 23° C. and 27° C. it was aerial from the beginning. In spite of the fact that this medium was favorable to growth the mycelium was delicate, uneven, and azonate at 23° C.; at 27° C. it was abundant but fine. At the highest temperature after 48 hours, it was delicate and fuzzy, but later became smooth and appressed. Conidia were present only in cultures maintained at 32° C. after 120 hours.

If rapid rate of growth of mycelium were a criterion for a good medium, Pfeffer agar might be considered one, for at 23° C. 12.66 mm. growth per day. and at 32° C. 13.33 mm. of growth was obtained, but as regards quantity of growth, Leonian and oat-

meal agars are far superior. The rate of growth on Pfeffer agar was rapid, but extremely delicate and neither zones nor conidia were present at any of the temperatures.

On oatmeal agar the slowest rate of growth, 8.33 mm., was observed at 23° C., and at 27° and 32° C. the same rate, 1.33 mm., was secured. The mycelium was aerial, though, even after 24 hours when the nodular character began to develop, and the mycelium became very dense and fluffy. Conidia were present at 23° C. after 168 hours and at 27° C. after 120 hours, although there were no zones.

TABLE X

DALDINIA Y (B. S. D.)

THE EFFECT OF DIFFERENT MEDIA AND DIFFERENT TEMPERATURES ON RADIAL GROWTH OF MYCELIUM

Medium	Temp. ° C.	Mm. of growth after hours				Rate of growth per day at 120 hrs. in mm.
		48	120	168	216	
Platanus decoction agar	23	2	33	55	PC	10.33
	27	4	34	PC	PCS	10.00
	32	5	35	PC	PCS	10.00
Leonian agar	23	2	24	49	PC	7.33
	27	20	PC	PCS	PCS	
	32	4	43*	PCS	PCS	13.33
Pfeffer agar	23	2	40	PC	PCS	12.66
	27	2	30	PC	PCS	9.33
	32	0	40	75	PC	13.33
Oatmeal agar	23	1	26	67*	PC	8.33
	27	16	20*	60	PC	1.33
	32	0	4	6	8	1.33

* = conidia present.
PC = plate covered.
PCS = plate and sides covered.

Daldinia vernicosa (D. Mo.).—In the two specimens of *D. vernicosa* the rate of growth exceeded that of the preceding species, and it was necessary to calculate the radial rate of growth per day after 48 hours. On *Platanus* agar the highest temperature seemed most favorable to rapid growth, for 15.5 mm. was secured, while at 27° C. the rate was only .5 mm. less; but at 23° C. it was considerably less, only 9.5 mm. per day. At 23° C. the mycelium was at first aerial, but after 48 hours it was prostrate. This was not the case at higher temperatures, for the mycelium was aerial.

Delicate, fuzzy, and uneven growth was characteristic at all the temperatures, and no conidia and no zones were formed.

A very rapid rate of growth, 16.5 mm. per day, occurred on Leonian agar at 32° C. The next highest temperature of 27° C. gave more rapid growth, 12.5 mm., than 23° C. where 11.0 mm. per day was secured. At all of the temperatures the mycelium was aerial except at 32° C. where at first it was prostrate, later becoming aerial. At 23° C. the mycelium was even and dense, while at higher temperatures it was uneven, delicate, and fuzzy. Even though no zones were formed at any of the temperatures, conidia were present at 23° C. after 120 hours, and not in cultures kept at 27° C. or 32° C.

TABLE XI

D. VERNICOSA (D. MO.)

THE EFFECT OF DIFFERENT MEDIA AND DIFFERENT TEMPERATURES ON RADIAL GROWTH OF MYCELIUM

Medium	Temp. ° C.	Mm. of growth after hours				Rate of growth per day at 48 hrs. in mm.
		48	120	168	216	
Platanus decoction agar	23	19	PC	PCHS	PCS	9.5
	27	30	95	PCHS	PCS	15.0
	32	31	PC	PCHS	PCS	15.5
Leonian agar	23	22	PC*	PCS	PCS	11.0
	27	25	PCS	PCS	PCS	12.5
	32	33	97	PCS	PCS	16.5
Pfeffer agar	23	30	PC	PCHS	PCS	15.0
	27	20	PC	PCHS	PCS	10.0
	32	17	PC	PCS	PCS	8.5
Oatmeal agar	23	13	55	PCHS	PCS	6.5
	27	17	41*	PCS	PCS	8.5
	32	20	35	68	PC	10.0

* = conidia present. PC = plate covered. PCS = plate and sides covered. PCHS = plate and half of sides covered.

On Pfeffer agar at 23° C. the rapid rate of growth of 15.0 mm. was secured, while at 27° C. 10 mm., and at 32° C. only 8.5 mm. of radial growth per day developed. After 48 hours the mycelium at 23° and at 27° C. was aerial, although it was appressed at first. At 32° C. it remained appressed.

At 32° C. 10 mm. of growth per day was observed to develop on oatmeal agar, while at 23° C. 6.5 mm., and at 27° C. 8.5 mm.

was obtained. Here again, oatmeal seemed least favorable to rapid growth, but the abundance of growth on this medium exceeded that on other media. It was typically aerial, at first even, then fluffy and nodular. At 23° and 27° C. it was azonate, but at 32° C. two zones were noted after 120 hours, and at 23° C. and 32° C. no conidia were noted, but at 27° C. after 120 hours conidia were present.

Daldinia vernicosa (C. Mass.).—At the three temperatures on *Platanus* decoction agar, the rates of growth per day were only .5 mm. apart, with the maximum of 11.5 at 23° C. At this temperature the mycelium was at first aerial, but after 48 hours, prostrate. At the two higher temperatures the mycelium was aerial. Even growth after 120 hours was characteristic of cultures maintained at 23° C. but at higher temperatures the growth was uneven. It was delicate, azonate, and no conidia were present.

TABLE XII

D. VERNICOSA (C. MASS.)

THE EFFECT OF DIFFERENT MEDIA AND DIFFERENT TEMPERATURES ON RADIAL GROWTH OF MYCELIUM

Medium	Temp. ° C.	Mm. growth after hours				Rate of growth per day at 48 hrs. in mm.
		48	120	168	216	
Platanus decoction agar	23	23	PC	PCS	PCS	11.5
	27	20	PC	PCHS	PCS	10.0
	32	21	PC	PCS	PCS	10.5
Leonian agar	23	17	PC	PCS	PCS	8.5
	27	29	PCS	PCS	PCS	14.5
	32	40	PCS	PCS	PCS	20.0
Pfeffer agar	23	14	PC	PCS	PCS	7.0
	27	16	PC	PCS	PCS	8.0
	32	33	PC	PCS	PCS	16.5
Oatmeal agar	23	4	25*	42	PC	2.0
	27	15	96*	PCS	PCS	7.5
	32	9	27*	52	PC	4.5

* = conidia present.
PC = plate covered.
PCS = plate and sides covered
PCHS = plate and half of sides covered.

A most rapid growth of mycelium was observed on Leonian agar, where 20.0 mm. per day developed at 32° C., while at 27° C. 14.5 mm., and at 23° C. only 8.5 mm. growth was obtained. Un-

even, aerial mycelium was secured at all temperatures, and while it was delicate and sparse at 23° C. at higher temperatures it was dense and fluffy. There were neither zones nor conidia.

The second highest rate of growth in this whole series was obtained on Pfeffer agar at 32° C. where 16.5 mm. of growth was secured. Only 7.0 and 8.0 mm. were secured at 23° and 27° C. respectively. Where the most rapid rate of growth occurred the mycelium was extremely delicate, uneven, and appressed; at 23° and at 27° C. it was aerial, even, the former delicate, the latter rather dense and fluffy at the outermost margin after 168 hours. In the three series the colonies were azonate and produced no conidia.

On oatmeal agar only 2.0, 7.5, and 4.5 mm. of growth per day was obtained at the temperatures in the ascending order of their intensities. Aerial, dense, and fluffy mycelium was noted at all temperatures, but the evenness became broken by nodular tufts after 120 hours when conidia occurred at the three temperatures. The higher temperatures induced zones to appear; at 23° C. there were two zones.

The close physiological relationship of *Daldinia Y* and *D. vernicosa* is indicated by the fact that these two species grow most rapidly on Leonian agar at 32° C., whereas the mycelium of *D. concentrica* responds most favorably on *Platanus* agar at 27° C. On the other hand, all three species produce the most abundant growth (as contrasted with the most rapid rate of growth) on oatmeal agar.

The nutrient values of the media employed in this study have been discussed above but there is an additional one here, oatmeal, which has not been previously described. The oatmeal, which was used in the preparation of the medium, was finely ground, then prepared in the usual manner. According to Wehmer ('11) the average percentage mineral content of *Avena sativa* grains is as follows: 3.2 ash, 30–40 SiO_2, 23–30 P_2O_5, 15–20 K_2O, 5–7 MgO, 2–4 CaO, 1–2.5 SO_3, minute amounts of Na_2O, and Cl and Cu. The analysis of the grain varies a great deal, but the percentages of the constituents given are: 12.8 H_2O, 10.25 nitrogenous substances, 5.27 fats, 59.68 nitrogen-free extractable material, 9.97 rough fiber, 3.02 ash, about 50–60 starch, and 2–5 sugar (sucrose)

and dextrin. Thus from the large quantity of carbohydrates, one may well see why the mycelium was so dense and fluffy in all of the species. It will be noted that where carbohydrates are abundant, the mycelium is aerial and becomes very nodular in the case of *D. vernicosa* and *Daldinia Y*, but very much less pronounced in *D. concentrica*. Another character which appears to be confined to oatmeal agar is the presence of conidia, for more conidia occurred on this medium than on any other. Since the two higher temperatures seem to be slightly more favorable than 23° C. the acceleration of the chemical activities by the higher temperatures may make it possible for the fungi to utilize carbohydrates more readily. Furthermore, it is possible that, aside from the carbohydrate, the nitrogen content, and the factor of temperature, the possible presence of vitamins in the oatmeal contributes to the luxuriant and abundant growth of mycelium. Growth is characteristically azonate at the higher temperatures and at the same time conidia are formed. It has been said of some fungi that zonation may be either induced by temperature or the proper food, but neither causes zonation here, evidently signifying that staling products are not localized concentrically.

The high carbohydrate content of Leonian agar is conducive to aerial and rather dense mycelium in all species. With one exception, *D. concentrica*, no zones were produced, but more conidia were observed on this medium than on any other except oatmeal agar.

Since Pfeffer agar contains no sugars, the growth of mycelium in all cases was very delicate, usually appressed and azonate with the exception of *D. concentrica*, where one zone and conidia were found. Evidently the abundance but not the rate of growth is dependent upon carbohydrates, as far as could be learned from petri dish cultures.

It is not surprising to find that *D. concentrica* grows more rapidly on *Platanus* decoction agar than any of the other species, for it will be remembered that this species in Missouri usually occurs on this host. It was surprising, however, to find that there were no conidia, even though two rather distinct zones were present.

Daldinia Y produces mycelium very similar in rate of growth, texture, and quantity to that of *D. vernicosa*, although the asco-

carp and ascospores are obviously closely related to *D. concentrica*. The behavior of *D. vernicosa* from the two different localities was very similar, as is seen by the two most rapid rates of growth that were obtained on Leonian agar at 32° C. Other characters were similar; dissimilarities were due probably to the differences in age and habitat. As a whole, 23° and 27° C. seemed to be most favorable for rapid growth of *D. concentrica* and its near relative, while for *D. vernicosa* 32° C. was more conducive to rapid growth.

Thus from these results it is demonstrated that the combined effect of medium and temperature upon mycelial development is of utmost significance in a comparative study of this kind. Such observations substantiate the statement of Coons, that: "The development of an organism is the resultant of the environment working upon definite internal potentialities of the organism and that with a given potentiality, the same external conditions call forth the same response with the constance of a chemical reaction."

THE EFFECT OF DIFFERENT HYDROGEN-ION CONCENTRATIONS ON THE RADIAL GROWTH OF MYCELIUM

Within the last few years no physiologist has considered that he has run the gamut of factors in any investigation until he has tested the relative acidity or alkalinity of the organism or the medium on which the organism grows. Especially for parasitic fungi, the hydrogen-ion concentration of the substratum has proved to be a factor in growth and development. Usually a slightly acid medium is favorable for the germination of spores, while for mycelial growth slight alkalinity is more favorable. In many cases, though, fungi have shown their ability to grow over wide ranges of hydrogen-ion concentrations and become adapted to a particular concentration if it is not absolutely toxic. MacInnes ('22) has briefly summarized the influence of hydrogen-ion concentration on many fungi, and she has demonstrated that the wheat scab organism is capable of growing over a wide range of hydrogen-ion concentrations.

In this experiment mycelium from single ascospore cultures of five-months-old material of *D. concentrica* (D. Mo.), *D. vernicosa* (D. Mo.), and *Daldinia X* (V. P. Mo.) was used. All of the asco-

TABLE XIII

THE EFFECT OF DIFFERENT HYDROGEN-ION CONCENTRATIONS ON THE RADIAL GROWTH OF MYCELIUM

pH	*D. concentrica* (D. Mo.)			*D. vernicosa* (D. Mo.)				*Daldinia X* (V. P. Mo.)		
	Millimeter growth in hours.									
	48	120	per day after 120	48	72	120	per day after 72	48	120	per day after 120
3.0	0	0	0	7.5	13.0	PC	1.88	.5	5.0	.9
3.4	0	0	0	10.5	25.0	PC	4.88	.5	7.0*	1.3
3.8	.5	10.0	1.9	15.5	28.0	PC	4.11	.5	17.0*	3.3
4.2	1.5	12.0	2.1	15.0	33.0	PC	6.00	2.0	20.5*	3.7
4.6	2.5	18.0	3.1	15.5	33.0	PC	5.88	2.5	27.0	4.9
5.0	2.5	16.5*	2.8	13.5	35.0	PC	7.11	2.5	30.0	5.5
5.4	2.5	17.5	3.0	14.5	34.0	PC	6.55	3.0	34.0	6.2
5.8	2.5	15.5*	2.6	13.5	34.0	PC	6.88	3.5	29.0	5.1
6.2	2.5	18.5*	3.2	14.0	33.0	PC	6.33	5.0	34.0	5.8
6.6	2.0	19.5*	3.5	11.5	24.0	PC	4.11	3.5	30.0	5.3
7.0	1.5	15.5	2.8	9.5	22.0	PC	4.11	5.0	31.0	5.2
7.4	1.5	12.0	2.1	6.0	20.0	PC	4.66	3.0	25.0	4.4
7.8	.5	.5	0	1.5	12.0	16.5	3.5	2.0	13.5*	2.3

* = conidia present. PC = plate covered.

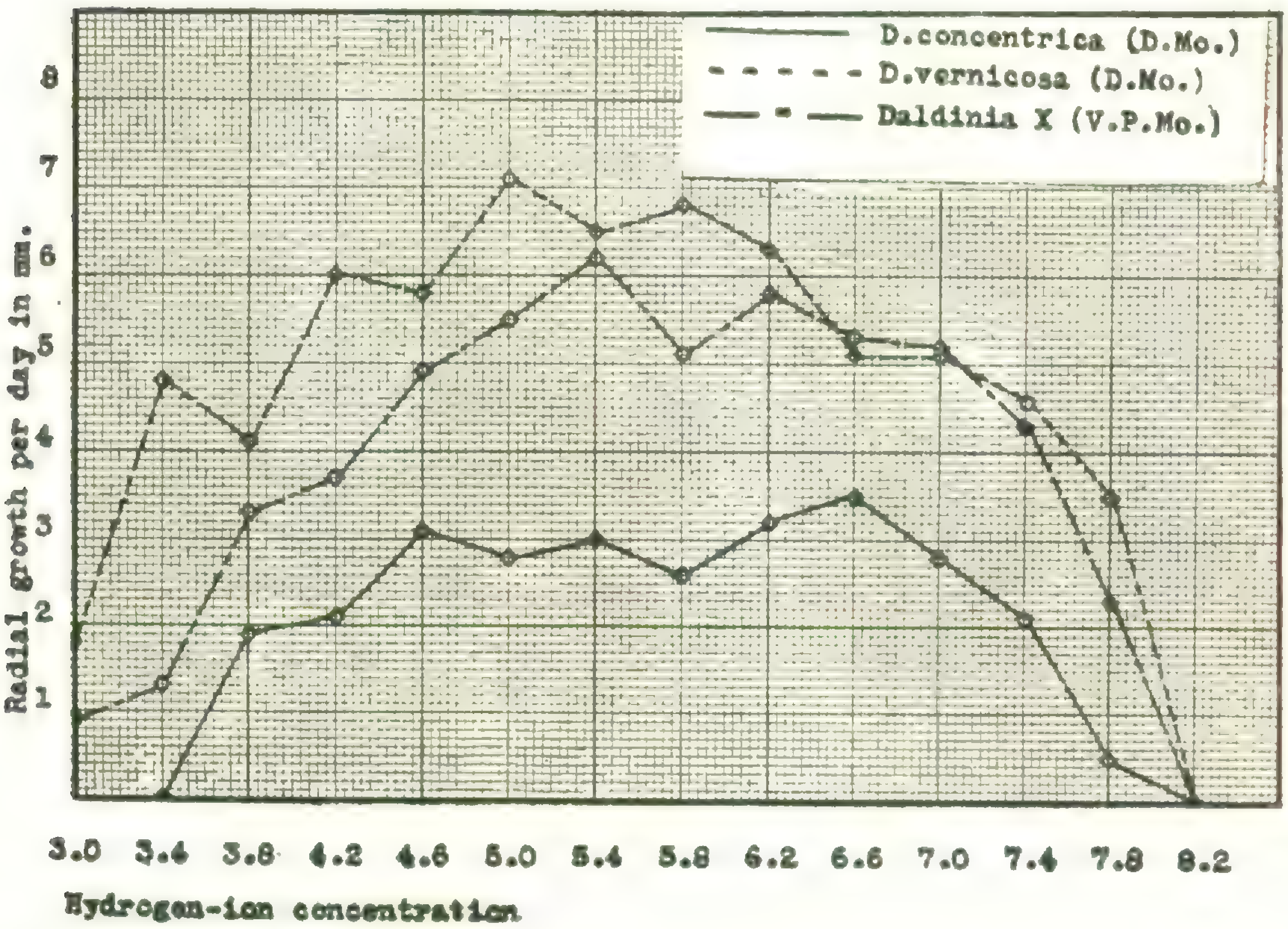


Fig. 4. The effect of different hydrogen-ion concentrations on mycelial growth.

spores had been frozen at $-5°$ C. for one and one-half months, then sprayed on Pfeffer solution agar, and single germinated ascospores were cut out and put on oatmeal-agar plates. Approximately same sizes, ¾–1 sq. cm., of actively growing mycelium were used as inocula, all of which were from stock cultures made up at the same time. Two different experiments were run and quadruple sets of each hydrogen-ion concentration were made, then an average taken. The range was from pH 3.0 through 7.8; at first pH 8.6 was included, but when no growth was obtained at this concentration it was omitted in the second experiment. Leonian agar was used and adjusted by citric acid and by NaOH. After inoculation the cultures were put into a darkened cabinet and maintained at room temperature. The results are given in table XIII, and the calculated radial growth per day is given in fig. 4 (see plate 36, figs. 3–5).

Daldinia concentrica.—Such extreme acid media as pH 3.0 and 3.4 are seen to be toxic to the mycelium of *D. concentrica*, for no growth was obtained at these two concentrations. The most rapid rate of growth was obtained at pH 6.6, where 3.5 mm. of growth per day was secured, and the slowest rate of 1.9 mm. was obtained at pH 3.8. Thus it seems that near neutrality is most favorable for rapid rate of growth. At pH 3.8 and 4.2 and 4.6, the mycelium was uneven, delicate, and rather prostrate; although one zone appeared at pH 4.6 after 120 hours, no conidia were present. The mycelium at pH 5.0 and 5.4 was even but prostrate and delicate; the former produced two zones and conidia after 120 hours, while the latter produced no conidia and was azonate. From pH 5.8 through 7.0, the mycelium was aerial, even, and rather dense; at pH 6.6 it was nodular, very dense, and fluffy, and conidia were present, but the colonies were azonate. At pH 6.2 the mycelium was not quite so fluffy, but in this case conidia were present. At pH 7.0, 7.4, and 7.8 the mycelium was uneven, delicate, and fuzzy; at the first one it was appressed and on the other two rather prostrate.

Daldinia vernicosa.—*D. vernicosa* not only grows rapidly but produces abundant mycelium. It was necessary to calculate the growth per day after 72 hours, since by 120 hours it had covered the plate. The minimum rate per day occurred at pH 3.0 where 1.88

mm. was obtained, while the maximum occurred at pH 5.0 where there was 7.11 mm. growth per day. As a whole the range from 4.2 through 6.2 was most favorable for rapid growth. From pH 3.0 through 4.2 the mycelium was appressed, even, and delicate; at pH 4.6, prostrate, and even, except for the outermost margin which was aerial and fluffy; from pH 5.0 through 6.2 it was characteristically aerial, even, and rather dense, except at pH 5.0 where it was less dense. At the remaining hydrogen-ion concentrations the mycelium was appressed, uneven, delicate, and fuzzy; at pH 7.8 it was very sparse. At no hydrogen-ion concentration did conidia or zones appear.

Daldinia X.—The mycelium of *Daldinia X* grew through the entire range of hydrogen-ion concentrations, but very slowly at pH 3.0 where only .9 mm. per day was calculated; the maximum occurred at pH 5.4 where 6.2 mm. of growth per day was observed. The optimum range was evidently from pH 5.4 through 7.0. At the first two concentrations the mycelium was appressed, fuzzy, and very delicate, but even. Conidia were present on pH 3.4 but not 3.0. On pH 3.8 and 4.2 the mycelium was even, rather aerial, dense, and fluffy; conidia were present in both cases. The mycelium was aerial, delicate, and fuzzy from pH 4.6 through 6.2, but rather dense and fluffy at pH 6.6, 7.0, and 7.4. On the most alkaline medium the mycelium was delicate and fuzzy with but a few conidia. There were from four to five zones after 72 hours on pH 6.2, 6.6, and 7.0, but no conidia. On pH 5.0 and 5.4 there were four and three zones respectively after the same length of time, but here, as in the preceding cases, no conidia were observed.

Thus compared, the differences in the three species are clearly distinct. The most abundant growth in the case of *D. concentrica* occurred within the narrow limits defined by pH 6.2 and 6.6; in the case of *D. vernicosa* at pH 5.4, 5.8, and 6.2, and in the case of *Daldinia X*, over a less acid range, from pH 6.6 through 7.4. Although the ascocarp and ascospores of *Daldinia X* and *D. vernicosa* are similar, the mycelium on these different hydrogen-ion concentrations looks very much more like *D. concentrica* than *D. vernicosa*. Another similarity is observed between *Daldinia X* and *D. concentrica* in the presence of conidia after 120 hours; the range in which they occurred was different, but in *D. vernicosa* they did not occur at all within this time limit of the experiment.

Brief Morphological Characters of the Ascocarp and Asexual Stage of the Forms Studied

In view of the physiological behavior of the forms it seems desirable to give at least a brief and superficial account of the gross morphology, since the physiological reactions of the fungi are so clearly correlated with the morphological characters. The

	D. concentrica	*Daldinia Y*	*D. vernicosa*	*Daldinia X*
Ascocarp				
External color	"Hays Brown" to "Dark Vinaceous Brown"	Dull black to bronzed black	"Hays Brown," becoming black and strongly laccate	"Snuff" to "Verona Brown"
Surface	Moderately papillate to base	Prominently papillate to base	Minutely papillate half way to base	Minutely reticulate on top. Zones prominent on stipe
Shape and size	Single or confluent, hemispherical. Size variable, 1–6 cm. diam.	Single, hemispherical, 2–4 cm. diam.	Usually single, substipitate, spherical, clavate, 1–3 cm. diam. above stipe	Confluent or single, substipitate in cross-section, elongate-elliptical or circular in young forms, .5–1.5 cm. diam.
Internal color	"Drab Gray" zones alternating with "Bone Brown"	"Benzo" zones alternating with "Fuscous"	Thin black zones alternating with wider "Pale Dull Gray"	Thin black zones alternating with wider "Pale Dull Gray"
Texture	Soft, persistent, and compact	Soft, persistent, and compact	Fragile, coalescing to produce irregular cavities, collapsing	Fragile, coalescing to produce irregular cavities, collapsing, more persistent than in *D. vernicosa*
Asexual				
Conidiophore size	3.2 μ diam.	2–2.2 μ diam.	2–2.2 μ diam.	4.8 μ diam.
Conidia shape and color	Singly or in whorls, ellipsoidal, hyaline	Singly or in whorls, ellipsoidal, hyaline	Singly or in whorls, ovoid to ellipsoidal, hyaline	Singly or in whorls, elongated, elliptical, hyaline
Size	2.4–3.2 x 4.8–6.4 μ	2–3 x 4–6 μ	2.4–3.2 x 2.4–3.2 μ	8–12.8 x 4.4 μ

descriptions are superficial, because more exact descriptions are to follow in a monographic study. The table is intended to emphasize the main differences only.

Summary

1. In these investigations, factors influencing the germination of ascospores and the development of mycelium of *D. concentrica*, *D. vernicosa*, and two unnamed species, *Daldinia X* and *Daldinia Y*, have been studied comparatively in pure culture.

2. It was found in most cases that ascospores over a year old failed to germinate either because of age or as a result of treatment with fumigants.

3. In experiments devised to determine the effects of oxygen, three sources were used: oxygen produced by the photosynthetic process of the alga, *Pleurococcus* sp., hydrogen-peroxide, and compressed oxygen. Germination of ascospores, both frozen and unfrozen of *D. concentrica*, was stimulated by oxygen from the first and last source. Ascospores of *D. vernicosa*, however, appeared to thrive better in the absence of oxygen artificially supplied. In both species, when germination occurred, growth of the germ-tubes appeared to be stimulated. Ascospores of *Daldinia X* were indifferent to the oxygen treatment.

4. Neither the ascospores of *D. concentrica* nor *D. vernicosa* germinated in pepsin solutions from .1 to 10 per cent.

5. Ultra-violet rays (578–289 $\mu\mu$) definitely stimulated germination of both frozen and unfrozen ascospores of *D. concentrica*. Maximum germination of *D. vernicosa* (4 per cent) was secured from unrayed but frozen ascospores; raying slightly favored germination of unfrozen ascospores. Frozen and unfrozen ascospores of *Daldinia X* were adversely affected by raying.

6. Ascospores of *D. vernicosa* and *Daldinia X* frozen for 3 months at —5° C. were stimulated to increased germination, whereas the opposite effect resulted when those of *D. concentrica* were similarly treated.

7. Ascospore germination of *D. vernicosa* was markedly stimulated by short exposures to high temperatures previous to inoculation, and although the percentages of germination increased as the temperatures were lowered, even at 100° C. more germination

was obtained than in the controls. Similar treatment of ascospores of *D. concentrica* resulted in a decrease in germination. In both species it seems that short exposures at 90° C. have approximately the same effect as lower temperatures (70–75° C.).

8. Ascospores of *D. concentrica* on oatmeal, Leonian, Pfeffer, prune decoction, and *Platanus* decoction agars subjected to a temperature of 38° C. for 24 hours did not germinate at all or only poorly, but when changed to 25° C. recovered from partial plasmolysis or increased in percentage of germination. Pfeffer agar was the most favorable medium for germination.

9. The effect of these same media on ascospore germination of *D. concentrica* at room temperature was a maximum percentage on Pfeffer agar and a minimum on prune-decoction agar. For *D. vernicosa* and *Daldinia X* the maximum germination occurred on Pfeffer agar and the minimum on *Platanus* decoction agar.

10. In maltose solutions the maximum germination of one-year-old ascospores of *D. concentrica* was obtained in 10 per cent concentration, while the minimum was obtained in .06 per cent. The maximum germination of the month-old ascospores was obtained in 10 per cent solution, while the minimum was obtained in .05 per cent. The younger ascospores were more consistent in their behavior than the older ones. Obviously the ascospores of *D. vernicosa* were benefited by this rest of a year, for their germination far exceeded that of the month-old ascospores. The maximum germination of the former was 17.3 per cent, which occurred in a 3 per cent maltose solution, while that of the latter was 4 per cent germination secured at 10 per cent solution. Ascospores of *Daldinia X* 2 months old did not germinate in any of the concentrations.

11. After 48 hours on a medium of pH 5.6 ascospores of *D. concentrica* gave 70 per cent germination and a minimum of 23 per cent at pH 2.4; the optimum range was from pH 4.8 through 6.0. Conidia occurred at 10 different hydrogen-ion concentrations, while in *D. vernicosa* they occurred at only 5 different ones. The maximum germination, 17 per cent, occurred at pH 4.8, and the minimum, 4 per cent, at pH 2.4; the optimum occurred between pH 4.8 and 6.4.

12. For the effect of light and darkness on growth of mycelium,

oatmeal agar gave more abundant growth than Pfeffer agar. In both cases, darkness was more conducive to more rapid aerial and abundant growth than light. In the case of *D. concentrica*, only slight changes in color occurred, while in the light decided changes were noted. A red secretion appeared both in *D. vernicosa* and *Daldinia Y*, of which the mycelia closely resemble each other in pure culture.

13. In determining the effect of different temperatures and media on the growth of mycelium, Pfeffer agar proved to be the best medium for rapid growth of *D. concentrica*, *D. vernicosa* (D. Mo.) (C. Mass.), and *Daldinia Y*, but oatmeal agar induced much more abundant mycelium. Thirty-two degrees C. proved to be the most favorable temperature for *D. vernicosa* and *Daldinia Y*, while 23° C. proved to be most favorable for *D. concentrica*. More conidia were found on media rich in carbohydrates. Neither zoning nor the presence of conidia was dependent on differences of exposure to light.

14. As to the influence of different hydrogen-ion concentrations on the growth of mycelium of *D. concentrica*, a very narrow range of pH 6.2 and 6.6 produced the most abundant growth; the most rapid rate of growth, 3.5 mm. per day, occurred at pH 6.6. The most abundant growth of mycelium of *D. vernicosa* occurred in the range of pH 5.4, 5.8, and 6.2, but the fastest rate of growth, 7.11 mm., occurred at pH 5.0. This was the most rapid-growing mycelium of all three species. The range in which the most abundant growth of mycelium of *Daldinia X* was produced was pH 6.6 through 7.4, but the most rapid rate per day, 6.2 mm., occurred at pH 5.4. Although the ascocarp and ascospores of *Daldinia X* closely resemble *D. vernicosa*, in pure culture the behavior in regard to mycelium and conidia is very similar to that of *D. concentrica*.

15. These experiments definitely indicate that the physiological reactions of the fungi are correlated with their morphological characters.

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Bibliography

Benecke, W. ('95). Die zur Ernährung der Schimmelpilze nothwendigen Metalle. Jahrb. f. wiss. Bot. **28**: 487–530. 1895.

Bisby, G. R. ('25). Zonation in cultures of Fusarium sulfureum. Mycologia **17**: 89–97. 1925.

Boudier, E. ('69). Memoire sur les Ascoboles. Ann. Sci. Nat. Bot. V. **10**: 191–268. 1869.

Brefeld, O. ('91). Untersuchungen aus dem Gesamtgebiete der Mykologie. **9**: 113; **10**: 337–339. 1891.

Brooks, F. T. ('13). Observations on pure cultures of some Ascomycetes and Basidiomycetes. Brit. Myc. Soc. Trans. **4**: 245–246. 1913.

Brown, W. ('23). Experiments on the growth of fungi on culture media. Ann. Bot. **37**: 105–129. 1923.

Bullot, E. ('97). Sur la croissance et les courbes du Phycomyces. Soc. Microsc. d. Belge, Ann. **21**: 84. 1897.

Clark, J. F. ('99). On the toxic effect of deleterious agents on germination of certain filamentous fungi. Bot. Gaz. **28**: 289–327, 378–402. 1899.

Constantineau, J. C. ('06). Über die Entwicklungsbedingungen der Myxomyceten. Ann. Myc. **4**: 495–540. 1906.

Coons, G. F. ('16). Factors involved in the growth of pycnidia formation of Plenodomus fuscomaculans. Jour. Agr. Res. **5**: 713–766. 1916.

De Bary, A. ('87). Comparative morphology and biology of the fungi, mycetozoa and bacteria. p. 350. Oxford, 1887.

Dodge, B. O. ('12). Methods of culture and the morphology of the archicarp in certain species of the Ascobolaceae. Torrey Bot. Club Bull. **39**: 139–197. *pl. 10–15*. 1912.

Duggar, B. M. ('01). Physiological studies with reference to the germination of certain fungous spores. Bot. Gaz. **31**: 38–66. 1901.

Elliot, J. S. B. ('20). On the formation of conidia and growth of stroma of Daldinia concentrica. Brit. Myc. Soc. Trans. **6**: 269–273. *pl. 6. f. 31–39*. 1920.

Ellis, J. B., and Everhart, B. M. ('92). The North American Pyrenomycetes. pp. 660–662. *pl. 38, f. 6–11*. 1892.

Eriksson, J. ('95). Über die Förderung der Pilzsporenkeimung durch Kälte. Centralbl. f. Bakt. Abt. II. **50**: 557–565. 1895.

Ferguson, M. C. ('02). Germination of spores of Agaricus campestris and other

Basidiomycetous fungi. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 16: 1–43. *pl. 1–31.* 1902.

Fraser, H. C. I. ('07). On the sexuality and development of the ascocarp in Lachnea stercorea. Ann. Bot. **21**: 349–360. 1907.

Gilbert, F. A. ('28). A study of the method of spore germination in the Myxomycetes. Am. Jour. Bot. **25**: 345–351. 1928.

Gillespie, L. J. ('18). The growth of the potato scab organism at various hydrogen-ion concentrations as related to the comparative freedom of acid soils from the potato scab. Phytopath. **8**: 257–269. 1918.

Grantz, T. ('98). Über den Einfluss des Lichtes über die Entwickelung einiger Pilze. Leipzig, 1898.

Haberlandt, F. ('78). Über den Einfluss des Frostes auf gequollene Leinsamen und die daraus gezogen Leinpflanzen. Landwirtsch. Versuchs-Stat. **21**: 357. 1878.

Hartig, R. ('85). Der ächte Hausschwamm Merulius lacrymans. Die Zerstörungen des Bauholzes durch Pilze. Berlin, 1885.

Hoffman, H. ('60). Untersuchungen über die Keimung der Pilzsporen. Jahrb. f. wiss. Bot. **2**: 267–337. *pl. 26–35.* 1860.

Jahn, E. ('05). Myxomycetenstudien IV: Die Keimung der Sporen. Ber. d. Deut. Bot. Ges. **23**: 489–497. 1905.

Janczewski, E. ('71). Morphologische Untersuchungen über Ascobolus furfuraceus. Bot. Zeit. **29**: 257–262; 271–278. *pl. 4.* 1871.

Klebahn, J. ('02). Kultur Versuche mit Rostpilzen. XI. Bot. Staatsinst. Hamburg, Mitt. Abt. 2. 20: 1–56. 1902.

————, ('05). Kultur Versuche mit Rostpilzen. XII. Zeitscher. f. Pflanzenkr. **15**: 65–108. *pl. 3.* 1905.

Klebs, G. ('96). Die Bedingungen der Fortpflanzung bei einigen Algen und Pilze. Jena, 1896.

————, ('00). Einige Ergebnisse der Fortpflanzungs-Physiologie. Ber. d. Deut. Bot. Ges. **18**: 201–215. 1900.

Lender, A. ('96). Des influences combinées de la lumière et du substratum sur le développement des champignons. Ann. Sci. Nat. Bot. VIII. **3**: 1–64. 1896.

Leonian, L. ('24). A study of factors promoting pycnidia formation in some Sphaeropsidales. Am. Jour. Bot. **11**: 19–50. 1924.

Mac Innes, Jean. ('22). The growth of the wheat scab organism in relation to hydrogen-ion concentration. Phytopath. **12**: 290–294. *f. 1.* 1922.

Maneval, W. W. ('26). Parasitic and wood-destroying fungi of Boone Co., Mo. Univ. Mo. Studies 1. 1926.

Massee, G., and Salmon, E. S. ('01). Researches on coprophilus fungi. I. Ann. Bot. **15**: 313–357. 1901.

————, ('02). *Ibid.* II. *Ibid.* **16**: 57–94. 1902.

McClatchie, A. J. ('94). Notes on germinating myxomycetous spores. Bot. Gaz. **19**: 245–246. 1894.

Miller, J. ('28). Biologic studies in the Sphaeriales, II. Mycologia **6**: 328–329. 1928.

Molliard, M. ('04). Forme conidienne de Daldinia concentrica. Soc. Myc. de France, Bull. **20**: 55–60. *pl. 6, f. 1–16.* 1904.

Molisch, H. ('94). Die mineralische Nahrung der niedern Pilze. 1894.

Möller, A. ('01). Phycomyceten und Ascomyceten. In Schimper A. F. W., Bot. Mitth. aus den Tropen, Heft 9. Jena 1901.

Müller-Thurgau, H. ('85). Beitrag zur Erklärung der Ruheperioden der Pflanzen. Landwirtschaft. Jahrb. **14**: 851–907. 1885.

Panisset, Thérèse E. ('29). Daldinia concentrica attacking the wood of Fraxinus excelsior. Ann. Appl. Biol. **16**: 400–421. *f. 1–22.* 1929.

Reed, H. S., and Crabill, C. H. ('15). The cedar rust disease caused by Gymnosporangium Juniperi-Virginianae Schw. Virginia Agr. Exp. Sta. Tech. Bull. 9: 1–106. 1915.

Robinson, W. ('26). The conditions of growth and development of Pyronema confluens, Tul. (P. omphaloides (Bull.) Fuckel). Ann. Bot. **40**: 245–276. 1926.

Saccardo, P. A. ('82). Sylloge fungorum Pyrenomycetes. **1**: 393–395. 1882.

Skupienski, F. X. ('22). Recherches sur le cycle evolutif de certains Myxomycetes. Paris, 1922.

Stameroff, K. ('97). Zur Frage über den Einfluss des Lichtes auf das Wachstum der Pflanzen. Flora **83**: 135. 1897.

Stevens, F. L. ('98). The effect of aqueous solutions upon germination of fungous spores. Bot Gaz. **26**: 377–406. 1898.

————, ('28). The effect of ultra-violet radiation on various fungi. *Ibid.* **6**: 210–225. 1928.

Ternetz, C. ('00). Protoplasmabewegung und Fruchtkörperbildung bei Ascophanus corneus Pers. Jahrb. f. wiss. Bot. **25**: 273–309. 1900.

Tulasne, L. R., et C. ('63). Selecta carpologia fungorum **2**: 31–33. *pl. 13, f. 11–16.* Paris, 1863.

Van Tieghem, P. ('76). Sur le développement du fruit des Ascodesmus, genre nouveau de l'ordre des Ascomycètes. Soc. Bot. France, Bull. **23**: 271–279. 1876.

Webb, R. W. ('19). Studies in the physiology of the fungi. X. Germination of the spores of certain fungi in relation to hydrogen-ion concentration. Ann. Mo. Bot. Gard. **6**: 201–222. 1919.

————, ('21). Studies in the physiology of the fungi. XV. Germination of the spores of certain fungi in relation to hydrogen-ion concentration. *Ibid.* **8**: 283–341. 1921.

Wehmer, C. ('11). Die Pflanzenstoffe, botanisch-Systematisch bearbeitet chemische Bestandteile und Zusammensetzung der einzelnen Pflanzenarten. Rohstoffe und Produkte. Phanerogamen. Jena, 1911.

Wolpert, F. S. ('24). Studies in the physiology of the fungi. XVII. The growth of certain wood-destroying fungi in relation to the H-ion concentration of the media. Ann. Mo. Bot. Gard. **11**: 43–97. 1924.

Explanation of Plate

PLATE 36

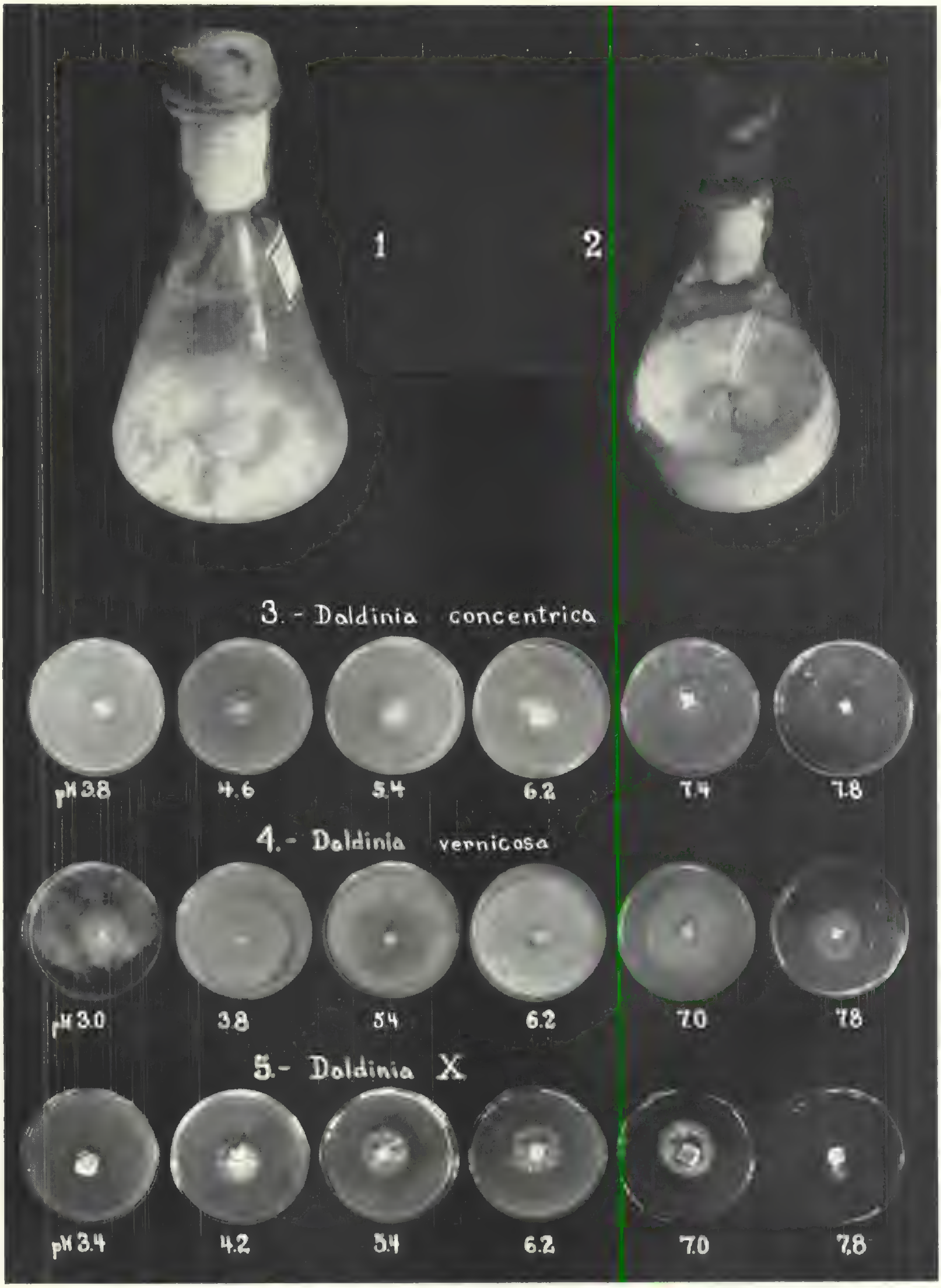
Fig. 1. The effect of *darkness* on the mycelial growth of *Daldinia Y* (B. S. D.) on oatmeal agar—after 30 days.

Fig. 2. The effect of *light* on the mycelial growth of *Daldinia Y* (B. S. D.) on oatmeal agar—after 30 days.

Fig. 3. The effect of different hydrogen-ion concentrations on the rate of growth of mycelium of *D. concentrica* (D. Mo.) 72 hours after inoculation. The numerous small blotches on the agar plates are not due to contamination but to undissolved bits of agar.)

Fig. 4. The effect of different hydrogen-ion concentrations on the rate of growth of mycelium of *D. vernicosa* (D. Mo.) 72 hours after inoculation.

Fig. 5. The effect of different hydrogen-ion concentrations on the rate of growth of mycelium of *Daldinia X* (V. P. Mo.) 72 hours after inoculation.



CHILD—DALDINIA

Explanation of Plate

PLATE 37

All figures were drawn with the aid of the camera-lucida, and were made from pure-culture material mounted in lacto-phenol cotton-blue.

Fig. 1. Ascospore of *D. vernicosa* (C. Mass.), showing the dark brown spore and the roughened nearly hyaline exospore. Drawn 24 hours after inoculation on bean-sprout agar. × 498.

Fig. 2. Ascospores of *D. vernicosa* (C. Mass.), showing the dark brown spore and the cracked mesospore. Drawn 24 hours after inoculation on bean-sprout agar. × 498.

Fig. 3. Germinated ascospores of *D. vernicosa* (D. Mo.). Drawn 24 hours after inoculation on Pfeffer agar. × 498.

Fig. 4. Germinated ascospore of *D. vernicosa* (C. Mass.), showing the flattened end of the germ-tube which became arrested in its development. Previous to inoculation the ascospore was frozen in sterile distilled water for 13 days at −5° C. Drawn 14 days after inoculation on Pfeffer agar. × 498.

Fig. 5. Germinated ascospore of *D. vernicosa* (D. Mo.). Drawn 48 hours after inoculation on Pfeffer agar. × 498.

Figs. 6 and 7. Germinated ascospores of *D. vernicosa* (D. Mo.). Drawn 24 hours after inoculation on Pfeffer agar with *Pleurococcus* alga and water in bottom of cell. × 498.

Fig. 8. Germinated ascospore of *D. vernicosa* (D. Mo.). Previous to inoculation the ascospore was heated at 80° C. for 10 minutes. Drawn 48 hours after inoculation on Pfeffer agar. × 498.

Fig. 9. Germinated ascospore of *D. vernicosa* (D. Mo.). Drawn 48 hours after inoculation on Pfeffer agar. × 498.

Figs. 10 and 11. Ascospore of *D. concentrica* (D. Mo.), showing the sloughing-off exospore and the longitudinal cleft in the light brown mesospore through which the germ-tube emerges. Drawn 24 hours after inoculation on bean-sprout agar. × 498.

Fig. 12. Ascospore of *D. concentrica* (D. Mo.), showing the sloughing-off exospore and the longitudinal cleft in the endospore through which the germ-tube emerges. Drawn 24 hours after inoculation on Pfeffer agar. × 498.

Fig. 13. Immature conidiophore and conidia of *D. vernicosa* (D. Mass.) developed from single ascospore on oatmeal agar. Note that the conidia arise as terminal swellings of the hyphae. Drawn 28 days after inoculation. × 498.

Fig. 14. Immature conidiophores and conidia of *D. concentrica* (D. Mo.) developed from single ascospore culture on oatmeal agar. Drawn 7 days after inoculation. × 498.

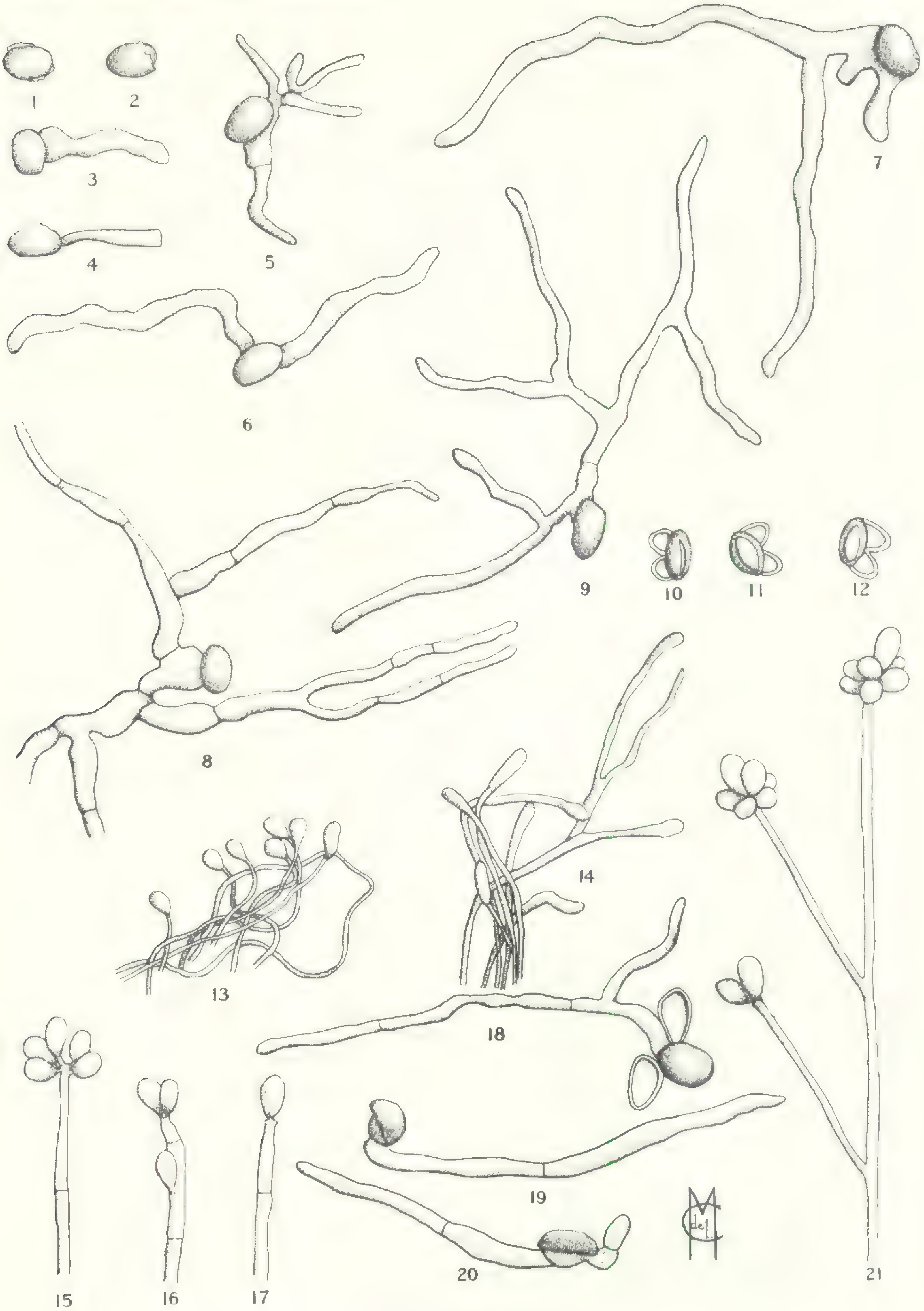
Figs. 15, 16, and 17. Mature conidiophores and conidia of *D. vernicosa* (C. Mass.) developed from single ascospore on oatmeal agar. Drawn 28 days after inoculation. × 498.

Fig. 18. Germinated ascospore of *D. concentrica* (D. Mo.). Drawn 24 hours after inoculation on Pfeffer agar with *Pleurococcus* alga and water in the bottom of the cell. × 498.

Fig. 19. Germinated ascospore of *D. concentrica* (D. Mo.). Previous to inoculation on bean-sprout agar the ascospore was heated to 100° C. for 2 hours. Drawn 10 days after inoculation. × 498.

Fig. 20. Germinated ascospore of *D. concentrica* (D. Mo.). Previous to inoculation on Pfeffer agar the ascospore was heated to 80° C. for 15 minutes. The characteristic splitting of the mesospore is shown. Drawn 48 hours after inoculation. × 498.

Fig. 21. Mature conidiophores and conidia of *D. concentrica* (D. Mo.) developed from single ascospore on Pfeffer agar. Drawn 17 days after inoculation. × 498.



CHILD—DALDINIA

Explanation of Plate

PLATE 38

Figs. 1 and 2. Germinated, very much swollen ascospores of *D. concentrica* (D. Mo.), showing the light brown mesospore and the hyaline endospore, developed on Pfeffer agar at pH 9.2. Drawn 19 days after inoculation. × 218.

Figs. 3 and 4. Germinated, very much swollen ascospores of *D. concentrica* (D. Mo.), showing the light brown mesospore and the hyaline endospore, developed on Pfeffer agar at pH 9.2. Drawn 19 days after inoculation. × 1071.

Figs. 5 and 6. Germinated ascospores of *D. vernicosa* (D. Mo.). Previous to inoculation on Pfeffer agar the ascospores were frozen at –5° C. for 38 days, then oxygen was run through the cultures at 6-hour intervals for 3 days. In fig. 6 the exospore, mesospore and endospore are evident. Drawn 120 hours after inoculation. × 218.

Figs. 7a and 7b. Swollen ascospores of *D. vernicosa* (D. Mo.) on Pfeffer agar at pH 2.6. Drawn 19 days after inoculation. × 1071.

Figs. 7c, 7d, and 7e. Mesospores cracked off. From ascospores on Pfeffer agar at pH 2.6. Drawn 19 days after inoculation. × 1071.

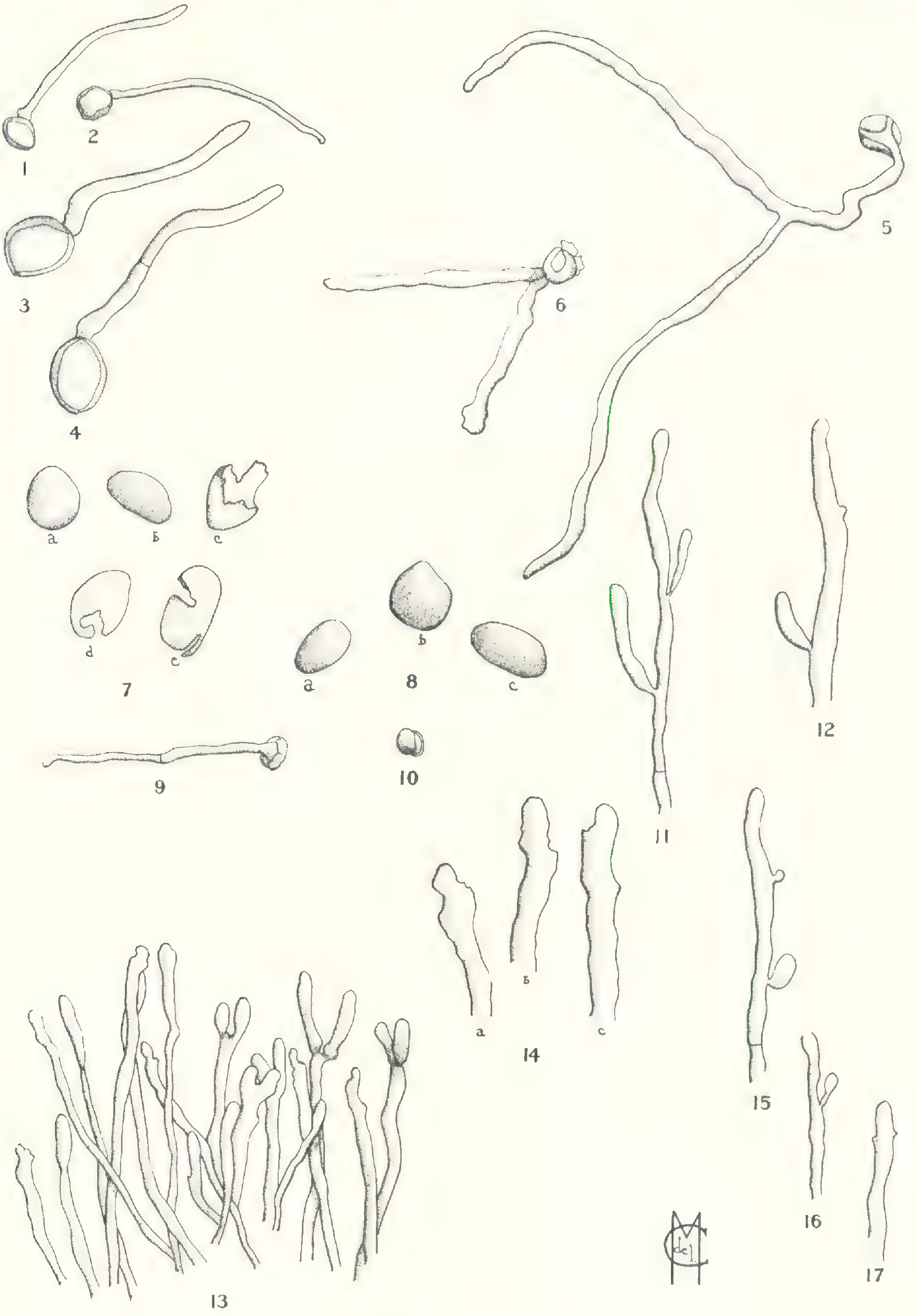
Figs. 8a, 8b, and 8c. Swollen ascospores of *Daldinia X* (V. P. Mo.). Previous to inoculation on Pfeffer agar, the ascospores were frozen at –5° C. for 3½ months. Drawn 24 hours after inoculation. × 1071.

Fig. 9. Germinated ascospores of *Daldinia X* (V. P. Mo.). Previous to inoculation on Pfeffer agar, the ascospore was frozen at –5° C. for 1½ months. Drawn 48 hours after inoculation. × 218.

Fig. 10. Ascospore of *Daldinia X* (V. P. Mo.), showing the sloughing-off exospore. Previous to inoculation on Pfeffer agar the ascospore was frozen at –5° C. for 1½ months. × 218.

Figs. 11, 12, 14a, b, c, and 15. Different stages of development of conidiophores and conidia of *Daldinia X* (V. P. Mo.), developed from a single ascospore on oatmeal agar. Drawn 120 hours after a bit of mycelium was transferred from the original culture to Leonian agar at pH 3.4. × 1071.

Figs. 13, 16, 17. Same as 11, 12, 14, and 15, but magnified × 218.



CHILD—DALDINIA

THE LIFE HISTORY AND CYTOLOGY OF SACCOBLASTIA INTERMEDIA, N. SP.

DAVID H. LINDER

Mycologist to the Missouri Botanical Garden
Assistant Professor of Botany in the Henry Shaw School of Botany of Washington University

The genus *Saccoblastia*, of the Auriculariales, was first described from Brazil by Möller ('95) from material that he had collected and studied. Subsequently several representatives of the genus have been described from Europe, and one from North Carolina in the United States. While its distribution is of interest, the real importance of the genus is emphasized by the amount of speculation as to the life history of its members, especially from the cytological point of view. For this reason, the writer has thought it well worth while to present his observations on an as-yet-undescribed species that he collected in Cuba.

The species of *Saccoblastia*, so far as can be determined from the literature, are all effused and fall into two groups,—those that are floccose or hypochnoid, and those that are of a gelatinous or mucous consistency. To this latter group, Bourdot and Galzin ('27) have applied the subgeneric name of *Saccogloea*, and it is to this subgenus that the species under discussion belongs. Both macro- and microscopically, however, it is distinct from all species that have been described up to the present time. For purposes of comparison, certain measurements of this and the related species have been tabulated. From the data thus presented, it is

Species	Probasidium	Basidium	Spores
S. sebacea	6–9 × 18–30 μ	4–6–9 × 45–75 μ	5–8 × 8–16 μ
S. sebacea var. *pruinosa*	7–9 × 12–18 μ	4.5–6 × 45–60 μ	4.5–7 × 6–10 μ
S. subardosiaca	7–9 × 30–36 μ	———	6.8 × 15–18 μ
S. caroliniana	8.5–16 × 24–45 μ	———	7–7.7 × 15–17 μ
Saccoblastia sp.	7.2–11 × 28–39.6 μ	5.4–9 × 64–72 μ	5.4–8.1–9 × 14–19.8–24 μ

clear that the Cuban material has a close resemblance to that from North Carolina, although differing in the size of the spores. A character not shown in the table, and one of great interest, is the presence of a second type of probasidium which is clavate and

resembles that of the genus *Iola*. This additional character, together with the fact that the colonies are not effuse but pustulate, makes it desirable to recognize this as a new species to which the name *Saccoblastia intermedia* is given because of the apparently transitional position between *Iola* and *Saccoblastia*.

Saccoblastia intermedia n. sp.

Fructifications pustulate, white to dilute brown, gelatinous to mucous, up to 1 cm. diam., becoming somewhat pendant at maturity. Context hyaline, the hyphae slender, 2.7–5.4 μ thick, without clamp connections. Probasidium of two types, the clavate type hyaline, rarely slightly constricted in the middle, 5.4–9 × (18)–36–45 μ, the walls slightly thickened; the lateral probasidium saccate, pendant, hyaline, 7.2–11 × 28–39.6 μ. Basidia hyaline, straight or slightly arcuate, 5.4–9 × 64.8–72 μ, 3–(5)-septate, bearing 4, less frequently as many as 6, sterigmata of varying length, 1.8–3.6 × 7.2–50 μ, the shorter ones conical. Basidiospores 1– rarely 2-celled, ellipsoid to elongate-ellipsoid, frequently concave on one side, tapering abruptly and obliquely to short truncate apiculi.

On moist decaying stump, Soledad, Cuba, September, 1924, *Linder* (TYPE in Farlow Herbarium, Herbarium of the Missouri Botanical Garden, and in the writer's herbarium).

Life History and Cytology

The material upon which the following account is based was preserved in alcohol of approximately 70 per cent strength. For study it was mounted in lactophenol to which had been added cotton blue and picric-nigrosin. The specimens as thus preserved in alcohol were plasmolyzed and the finer details of nuclear structure were lost. The lactophenol, however, practically restored the cytoplasmic structure, and as a result the nuclei in most of the material became clearly visible and were stained by the combination of cotton blue and picric-nigrosin.[1]

Examination of the pustules under the microscope reveals the fact that the fruiting body is not highly developed. The hyaline

[1] Weston, W. H. A useful modification of Amann's medium. Science N. S. **70**: 455. 1929.

hyphae growing out radially in the gelatinous matrix soon give rise to peculiarly twisted or irregularly waved hyphae that connect two or more of the main hyphae (pl. 39, fig. 2, and pl. 41, fig. 1). The walls of these connectives are somewhat thicker than are those of the remainder of the vegetative hyphae, and are also slightly, though distinctly, colored brown. The peculiar growth indicates that the junction of the two hyphae is more than a mere anastomosis and that the wavy development is in reality the result of a stimulus that is sexual in nature. In other words, the connectives appear to take the place of clamp connections. Additional credence is given to this supposition by the abundance of such hyphae in the region below the first-formed probasidia. This is clearly shown in pl. 39, fig. 2, where the clavate probasidia are formed immediately above the junction of the hyphae with the connective.

The clavate probasidia are produced terminally on hyphae or on the ends of branches from them, by swelling. At the initiation of probasidium formation the protoplasm in the region involved becomes dense, and the nuclei are clearly seen in pairs for the first time. As enlargement of the tip of the hypha proceeds, the paired nuclei increase slightly in size and then migrate into the now clavate body (pl. 41, figs. 2–4) where they shortly fuse. The resulting nucleus is larger and, with its more deeply staining nucleolus, is clearly visible.

Just as in the clavate type of probasidium, the saccate type is also the seat of nuclear fusion, the only difference being that the paired nuclei migrate laterally into the sac-shaped outgrowth from the main hypha as is shown in pl. 40, figs. 1–3, and pl. 41, figs. 5–7. The saccate probasidia, although produced concurrently with the clavate type, do not appear until later in the life history of the fungus. If, as has been assumed earlier in this paper, *Saccoblastia intermedia* is transitional between *Iola* and *Saccoblastia*, then it seems possible to assume the saccate probasidia to be a secondary type that allows proliferation, and is the type that has become fixed in the remaining species of *Saccoblastia*. Not infrequently, the growing point of the saccate probasidium, the base in the earlier stages of development, continues its growth by producing a germ-tube (pl. 40, fig. 4, and pl. 41, fig. 9)

in which case it appears to be transitional between the two types of probasidia. Also, although more rarely, the saccate type may germinate at the basal and apical end (pl. 41, fig. 10). Usually, however, such exceptions are infrequent, and the normal method of germination is by apical growth (pl. 41, fig. 8). At all events, the paired nuclei migrate laterally into the small immature probasidium and very quickly fuse. The rapidity with which this migration and fusion take place becomes evident when the sizes of the sacs, shown in pl. 41, figs. 5–7, are compared.

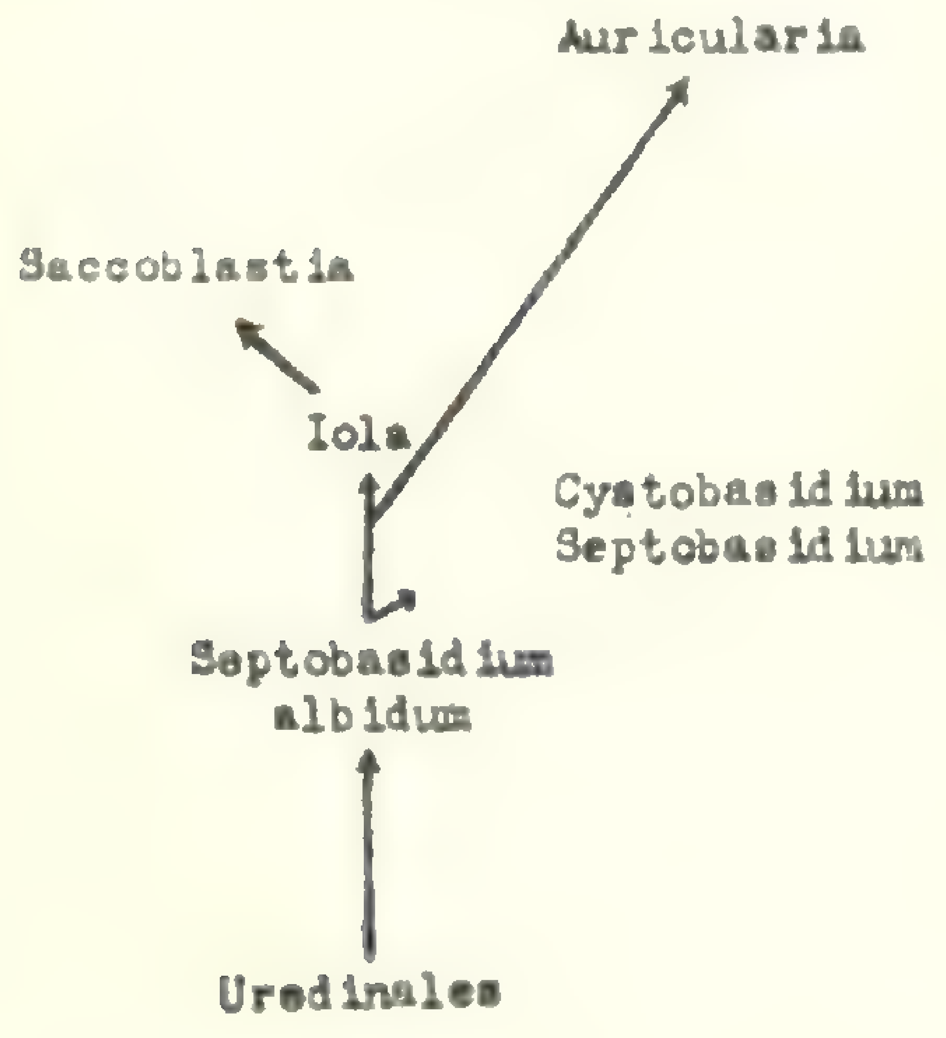
After a short rest, the probasidium sends forth a long hypha, or promycelium, which eventually enlarges terminally to become the true basidium. The fusion nucleus remains behind in the probasidium until the hypha attains full length, then there is a rapid migration of the nucleus into the basidium, followed by the entire protoplasmic contents of the probasidium and hypha (pl. 41, fig. 1). That the migration of the nucleus is rapid can only be inferred from the fact that the nucleus has never been observed by the writer anywhere but in the probasidium or the true basidium, never in the hypha connecting the two. Once the basidium is formed, it is most frequently 3-septate and each of the resulting cells has but a single nucleus. The nucleus and the protoplasmic content of each cell eventually migrate into the spore as it is formed so that the probasidium after it has produced the spores is nothing but an empty shell (pl. 39, fig. 1, and pl. 41, figs. 13 and 17).

Discussion

From the above account of the life history of this species it is obvious that, with the fusion of the paired nuclei taking place in the probasidium, that organ is actually homologous with the teleutospore of the rusts. Furthermore, the manner of germination of the basidium, that is, spore production, is strikingly like that found in the rusts. The resemblance between the probasidium and the teleutospore has been remarked upon since the genus *Saccoblastia* was first described. Möller ('95) in his account of the genus says: "Auch unter den Uredinaceen giebt es ja Formen, bei denen die Teleutospore ohne längere Ruhepause unmittelbar zur Basidie auskeimt. Durch diese Formen wird die nahe Ver-

wandtschaft unserer Saccoblastia-Arten mit den Uredinaceen besonders deutlich." Coker ('20) also mentions this relationship in the following extract from his account: "This genus reminds one strongly of the rusts, particularly the genus Gymnosporangium, where the teleutospore sprouts as soon as formed. If the relationship is as close as it seems the pear-shaped sac would be the homologue of the teleutospore. Note that this sac when long is constricted in the middle." While other writers point out this affinity, Coker is the only one who implies that the genus is derived from the rusts. Thus, Möller ('95), Neuhoff ('24), and Gäumann ('26), in their phylogenetic trees, indicate that this genus and the family to which it belongs, the Auriculariaceae, arose before the rusts. The main objection to Möller's scheme of evolution is based on the fact that in the Ustilaginaceae the nuclei in the cells of the basidium divide into two daughter nuclei, one of which migrates into the spore, the other remaining in the basidial cell. In *Saccoblastia* such is not the case, for the nucleus migrates into the spores with the protoplasm of the cell after the manner of *Gymnosporangium* or other members of the Pucciniaceae. To Neuhoff's and Gäumann's system it may be objected that a form with a relatively simple life-cycle should not be selected as the source of forms with a very complicated one.

From the nature of the subject, discussions of phylogeny are highly theoretical, yet it seems to the writer that the evidence pointing to the derivation of the Auriculariales from the Uredinales is stronger than the reverse. The evolutionary tendency seems to be from the rusts to *Auricularia* somewhat in the manner shown briefly in the accompanying text-figure. It is quite possible that the group as a whole is polyphyletic in its origin, but in this scheme the chief idea is to show trends in certain characteristics. Thus we find among the Pucciniaceae a tendency to drop out one or more steps in the life-cycle. Also, as is true in *Gymnosporangium*, there is a marked shortening of the



rest period of the teleutospore. If now it can be supposed that during the past history of the family, either through gradual evolution or through mutation, a race arose that was weakly parasitic or even saprophytic, then we arrive at the forerunner of a genus similar to *Septobasidium* or *Cystobasidium* in which the thickened walls of the probasidium still are in evidence. In this connection, it is unfortunate that Patouillard ('13) was unable to make a cytological study of the toruloid spores of *Septobasidium albidum*. Had careful investigation shown the spores to be binucleate, then there would have been demonstrated an even closer relation between the rusts and *Septobasidium* since in that case the toruloid spores might with reason be considered homologous with aecidiospores.

The next step in advance would be a genus similar to *Iola* of which the probasidium has practically lost its thickened walls. Through *Saccoblastia intermedia* with its clavate and saccate probasidia there appears to be a natural transition from *Iola* to *Saccoblastia*. The fact that the clavate probasidia are the first produced, and that they are found only in the older material, is significant. Since the clavate type is terminal, it is apparent that in order to produce additional probasidia with the least waste of material the subsequent probasidia must be produced laterally from the binucleate hyphae. This is what appears to have happened, but the remaining members of the genus *Saccoblastia* have retained the saccate type to the exclusion of the clavate.

Reduction of the probasidium is continued until in *Auricularia* we find, according to Gäumann and Dodge ('28, page 542), the place of fusion of the nuclei indicated only by a slight swelling. The branch of the family tree terminated by *Auricularia* appears to have arisen slightly before *Iola* since the latter genus apparently has lost the asexual method of reproduction. In *A. auricula-judae* the paraphyses have been shown by Sappin-Trouffy ('96) to be binucleate. These binucleate cells might be considered as homologous with the conidia produced by *Septobasidium albidum*, although they have lost their reproductive function. The binucleate condition of the spores of *S. albidum* would not be unparalleled, for Dangeard ('95) has shown the presence of binucleate oidia in *Dacryomyces deliquescens* of the Dacryomycetales. Should

the conidia of *S. albidum* or other species of *Septobasidium* eventually prove to be binucleate, then there would be slight reason for doubting the homology between such conidia and aecidiospores.

Throughout this theoretical discussion, it will be observed that the present hypothesis is founded on the reduction of the teleutospore or probasidium, on the reduction of the aeciospores, on the development of an extensive fruiting body, and finally on the transition from the parasitic mode of existence to the saprophytic. Still another phase of the subject that has been considered, though not discussed for lack of available knowledge, is the relation of the sporidia to pycnidiospores. Brefeld ('88), however, has remarked on the resemblance between the two, and has called attention to the fact that he was unable to obtain germination of the sporidia.

It is not necessary to consider the sporidia homologous with the pycnidiospores, although a study of the cytology and the relationship of these spore forms would undoubtedly bring to light much very interesting information. To the writer's way of thinking, it is sufficient to realize that the morphology of the basidiospores of the rusts and Auriculariales is fairly constant throughout the groups. Therefore, to find that the spores of certain rusts, such as *Cronartium ribicola*, also produce sporidia is sufficient evidence to show that there is a very close relationship between the two orders.

All factors considered, and in the light of present-day knowledge, it would appear that the Auriculariaceae are derived from the Uredinales through the reduction or degeneration of the reproductive organs as a result of the saprophytic mode of existence. To have the Uredinales derived from the Auriculariales would presuppose the development of potentialities in organs or even the development of the organs themselves. The probasidia of the Auriculariales have all the evidence of being vestigial structures handed down from the Uredinales, even though the latter order be derived from the Red Algae, the Zygomycetes, or even, as seems most probable, from a parasitic group of Ascomycetes.

Bibliography

Bourdot, H. et A. Galzin ('27). Hymenomycetes de France **1**: 4–5. 1927.

Brefeld, O. ('88). Unters. a. d. Gesammtgeb. d. Myk. **7**: 1–178. *pl. 1–11.* 1888.

Coker, W. C. ('20). Elisha Mitch. Scientif. Soc. Jour. **35**: p. 121. *pl. 33, 53.* 1920.

Dangeard, P. A. ('95). Le Botaniste **4**: 119–181. *figs. 6–7.* 1895.
Gäumann, E. ('26). Vergleich. Morph. Pilze. 626 pp. Jena, 1926.
————, and C. W. Dodge ('28). Comp. Morph. Fungi, 701 pp. New York, 1928.
Möller, A. ('95), in Schimper, Bot. Mitt. a. d. Tropen **8**: 1–179. *pl. 1–6.* 1895.
Neuhoff, W. ('24). Bot. Archiv **8**: 250–297. *pl. 1–4, 7 text-figs.* 1924.
Patouillard, N. ('13). Compt. Rend. Acad. Sci. Paris **156**: 1699–1701. *figs. 1–2.* 1913.
Sappin-Trouffy, P. ('96). Le Botaniste **5**: 53–58. *figs. 3–6.* 1896.

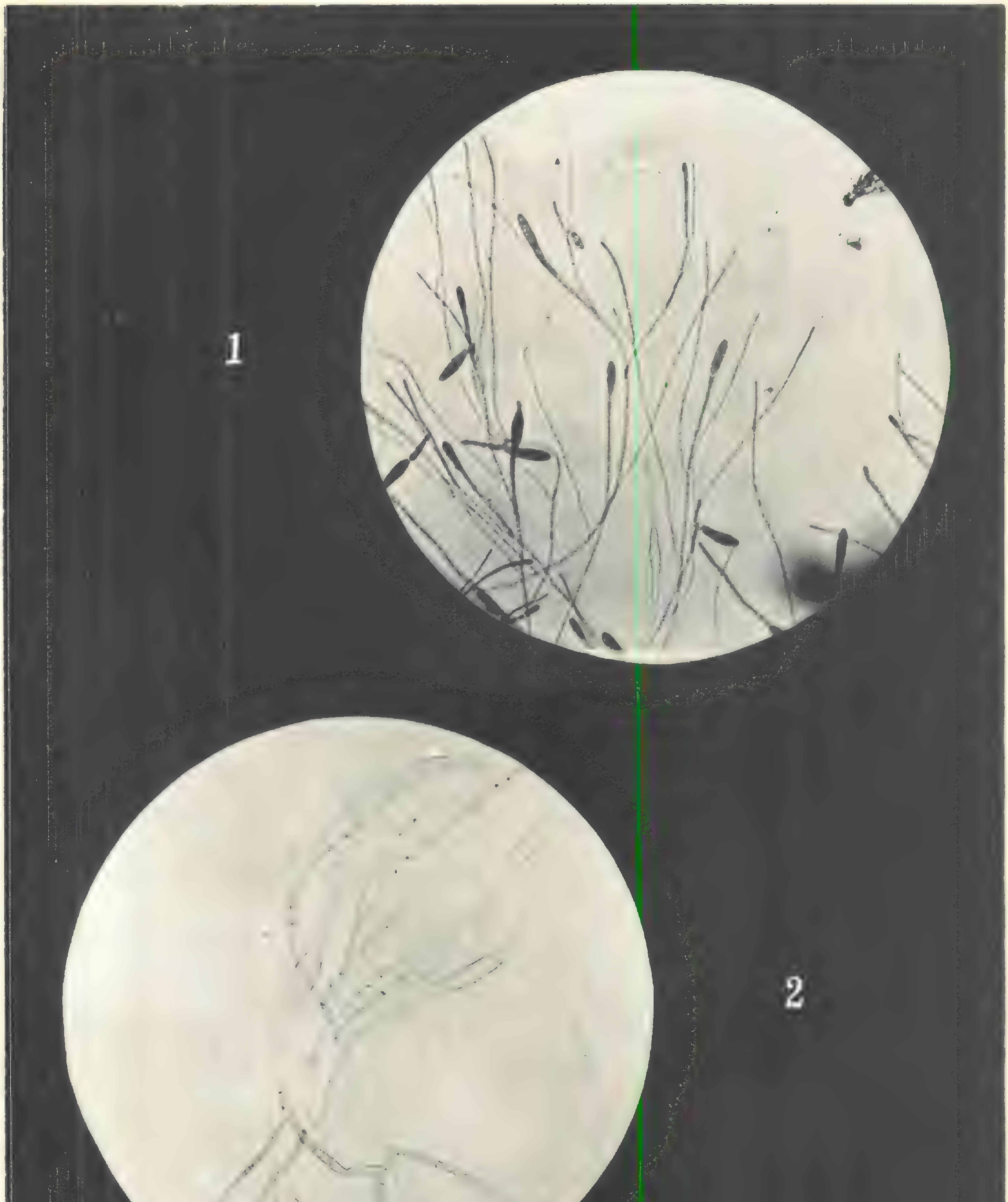
Explanation of Plate

PLATE 39

The material from which all photographs and drawings were made was mounted in Amann's lactophenol to which had been added cotton blue and picric-nigrosin. The photographs were made on Eastman panchromatic plates with the aid of a Wratten "A" (red) filter.

Fig. 1. Photograph at a low magnification to show the characteristic features of *Saccoblastia intermedia.* In the middle of the picture, near the bottom, will be seen an empty probasidium which has given rise to a true basidium, barely outlined above. The latter has been emptied of its contents through the production of basidiospores. An immature saccate probasidium with its fusion nucleus is shown to the left of the empty basidium, while immediately below the point of attachment of the probasidium, on the same hypha, are paired nuclei that have not fused. Below these are two nuclei that are approaching the paired condition. Approx. × 120.

Fig. 2. Clavate probasidia are shown arising after the fusion of the connective hypha with the main one. Paired nuclei may be observed in the hyphae between the two uppermost probasidia. Approx. × 240.



LINDER—SACCOBLASTIA

COCKAYNE, BOSTON

Explanation of Plate

PLATE 40

The magnification in all instances is approximately × 700.

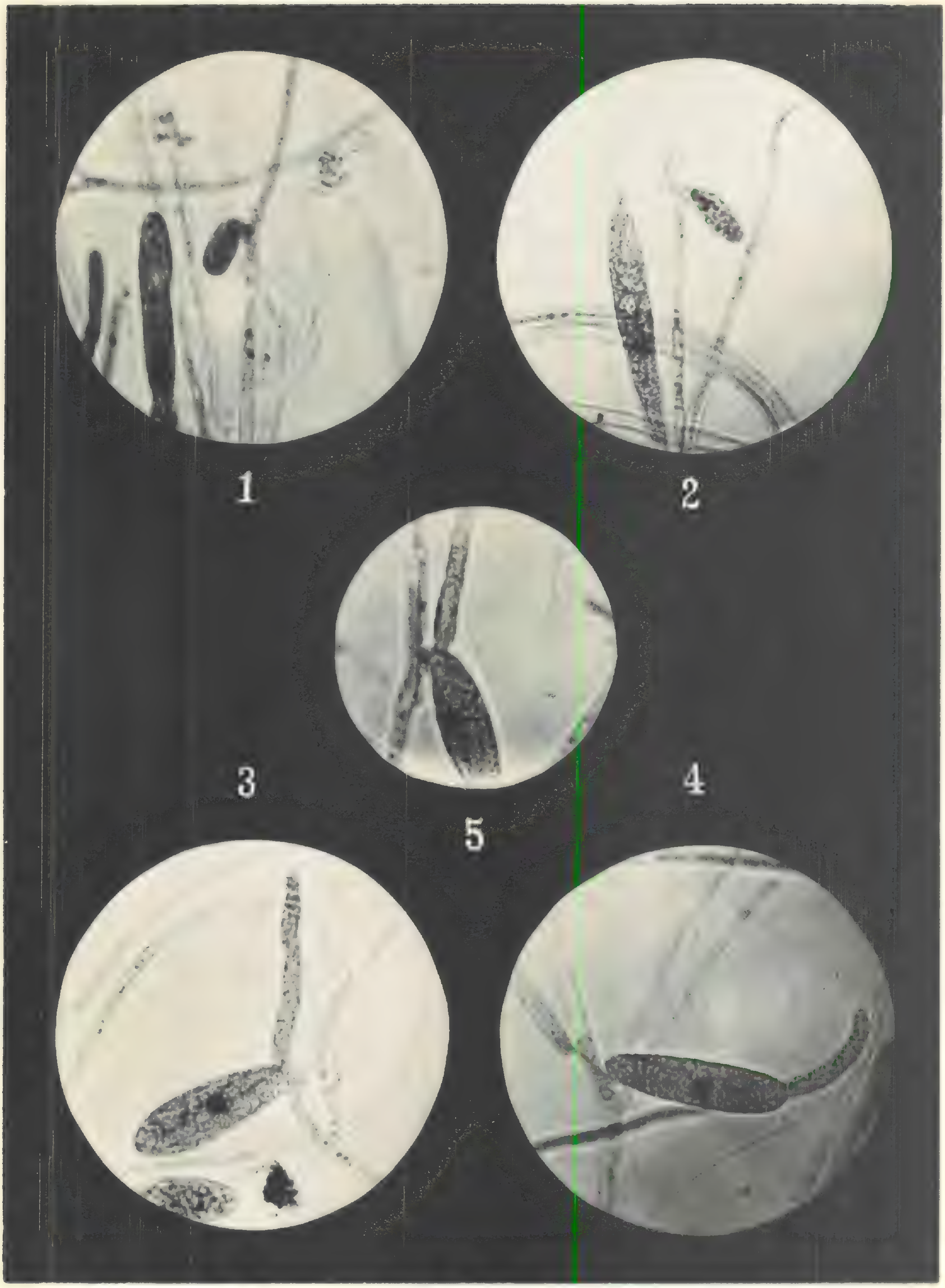
Fig. 1. A young probasidium into which one of the paired nuclei has migrated. The other nucleus is about to enter. Below and on the same hypha are two nuclei which have associated in pairs. See also pl. 41, fig. 5.

Fig. 2. A young probasidium in which the two nuclei have become closely associated and are about to fuse. See also pl. 41, fig. 6.

Fig. 3. A germinating probasidium with its conspicuous fusion nucleus.

Fig. 4. A probasidium continuing apical growth by the production of a promycelium from what is ordinarily the basal end.

Fig. 5. A germinating probasidium showing the conspicuous nucleus with its more deeply staining nucleolus. The promycelium is more than four times as long as this particular probasidium.



LINDER—SACCOBLASTIA

COCKAYNE, BOSTON

Explanation of Plate

PLATE 41

All drawings have been made with the aid of a camera lucida and are shown at a magnification of × 600.

Fig. 1. Shows the peculiarly wavy and somewhat twisted connective hypha that is formed prior to the production of probasidia. Such hyphae appear to take the place of clamp connections. See pl. 39, fig. 2.

Figs. 2–4. Formation of the clavate type of probasidium.

Figs. 5–8. Formation of the saccate type of probasidium. Figs. 5 and 6 are drawn from the same probasidia as are shown in pl. 40, figs. 1–2.

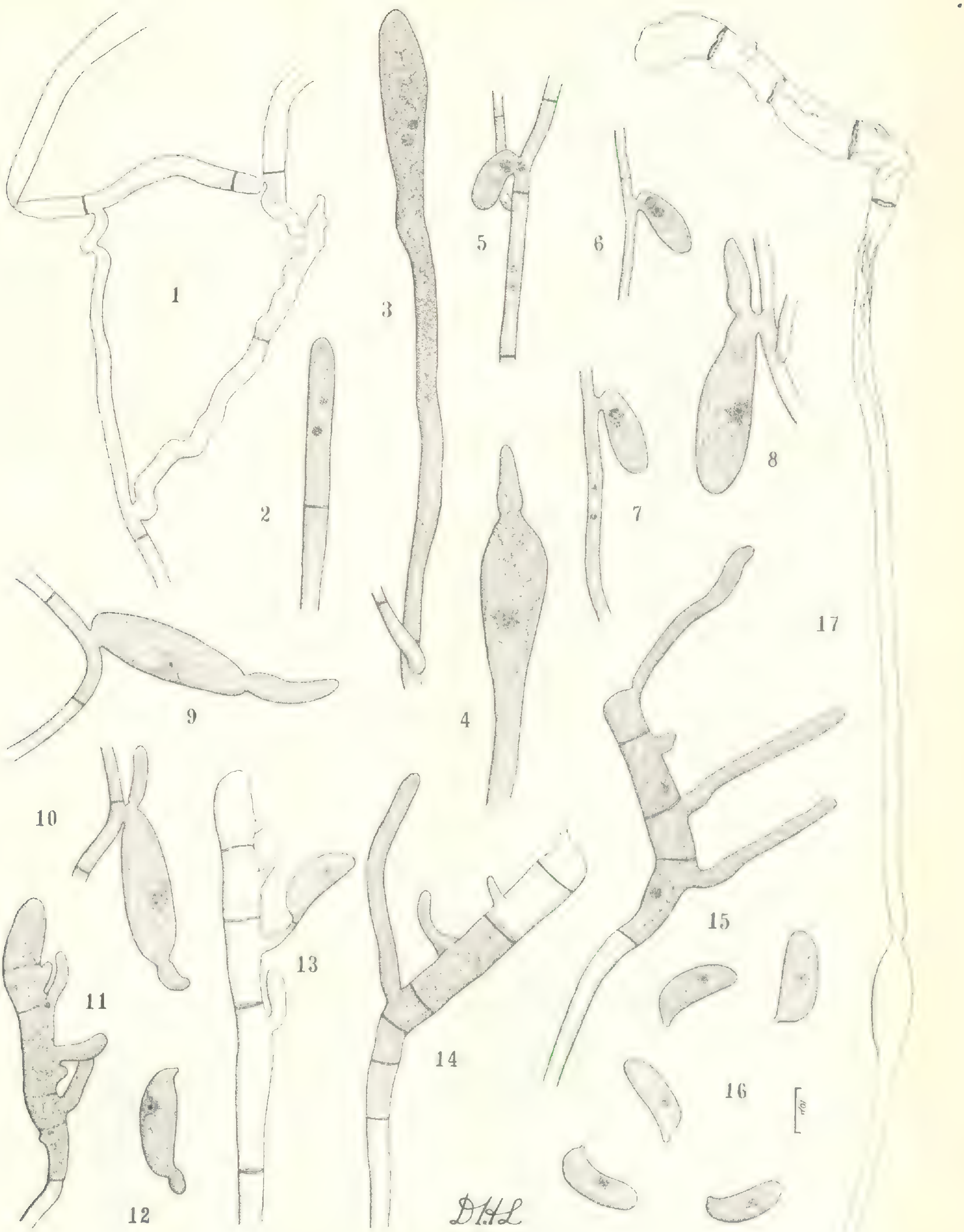
Figs. 9–10. The abnormal germination of probasidia. In fig. 9 the promycelium is arising from the basal end of the probasidium, while in fig. 10 each end is giving rise to a promycelium.

Figs. 11, 13–15. Types of true basidia. In fig. 13 spores have been produced but only one remains attached. It will be noted that not all of the protoplasm of the basidial cell has been able to enter the spore. In the remaining basidia are shown variations in the size of the sterigmata and number of septations of the basidia.

Fig. 12. A germinating basidiospore.

Fig. 16. Basidiospores, all of which contain but one nucleus apiece.

Fig. 17. A probasidium which has given rise to a promycelium and basidium. The promycelium is somewhat shortened After the basidium has produced the basidiospores, it collapses and finally disintegrates. Compare with that shown in pl. 39, fig. 1.



LINDER—SACCOBLASTIA

COCKAYNE, BOSTON

NON-SYMBIOTIC GERMINATION OF ORCHIDS

ROLAND V. LA GARDE

Research Assistant, Missouri Botanical Garden

The propagation of orchids from seeds is a problem which has attracted the attention of many investigators. That orchids could be grown in the greenhouse from seeds was not considered extraordinary; orchid growers in Europe and in this country were successful in this line of work. Naturally scientists took up the study of the conditions of germination. In the roots of the orchid plants symbiotic fungi had been detected, and the first investigators of this problem, Bernard ('09) and Burgeff ('09) undertook experiments with the symbiotic fungus. Since they had no success without the fungus, the presence of the fungus was considered to be a *conditio sine qua non.* In 1922 Knudson published the results of his successful experiments on the non-symbiotic germination of orchids, and a number of other investigators have worked on the same subject, in the majority of cases successfully. It is a well-known fact that a greater knowledge of the conditions for growing orchids is of particular interest not only to those working on the subject for commercial purposes, but also to those engaged in scientific investigations.

From Knudson's ('25, '27) experiments we learn that the metabolic processes of the fungus bring about chemical changes in the medium which make it more assimilable. Chemical compounds indigestible for the seedlings are broken up or transformed into ones which can be easily used as food by the embryo. Another favorable influence of the fungus is the gradual acidification of the medium, according to Burgeff, Knudson, and Clement. However, experiments showed that it need not be necessarily the special orchid fungus. Other fungi may produce the same effect. Every one dealing with the germination of orchid seeds will have made the same discovery. From the experiments of Knudson and other investigators, such as Constantin and Magrou ('22), Ramsbottom ('22), and Clement ('24, '26, '29), our present knowledge of the requirements for successful germination of

orchid seeds can be summed up as follows: a suitable solution of mineral salts, a satisfactory sugar supply, and a favorable hydrogen-ion concentration. These are conditions which can be obtained by a nutrient solution, the composition of which has been determined by previous investigations. This has been proved in a great number of experiments on seeds from different species of orchids, and there is no doubt that further investigations will show that the theory holds for all species of orchids. If we take into consideration these three main requirements, mentioned above, and determine, by changing the composition of the medium, the best conditions of germination, we will be able to give a list of the most favorable nutrient solutions for germinating seeds of each species of orchids.

In preliminary experiments nutrient solutions containing only sugars, three-times distilled water, and agar (Merck's Reagent) which had been washed for three weeks in thrice-distilled water and carefully dried in a desiccator over concentrated sulphuric acid, were used. Maltose, glucose, levulose, and saccharose (Merck Reagents) were used as sugar supplies. The best germination and growth of Cattleya seeds were recorded on nutrient media with maltose and at pH values between 4.8 and 5.4. The seedlings developed two leaves within five months and appeared healthy. Transplanted to full nutrient solutions with a suitable sugar supply development and growth continued as in seedlings germinated the usual way. The results prove the importance of carbohydrates in the germination of orchid seeds. For this reason the experiments with solid media were carried out and the results are reported here.

It is hoped that the experiments reported in this paper may be a contribution to the subject.

Methods

As culture vessels Erlenmeyer-flasks of "Pyrex" glass of 250-cc. capacity were used. One hundred cc. of nutrient agar was poured into each flask, the neck of the flasks closed with a cotton plug, and the flasks sterilized in an autoclave for 30 minutes under a pressure of 10 lbs. Then the medium was allowed to cool in a slanting position. The medium was so

adjusted before sterilization that when the process was concluded the desired pH resulted, as was shown by tests. All seeds were sterilized in chlorinated lime solution for 30 minutes, according to the procedure recommended by Wilson ('15). During this time the solution was shaken frequently to moisten all seeds. The sterilizing solution was then poured out and sterilized distilled water added under sterile conditions, and in this the seeds remained until they were planted on the agar slant with the aid of a sterilized platinum loop. After the seeds were planted, the cotton plug and the neck of the culture flask were covered with a double layer of waxed paper fastened with a rubber band to prevent too rapid an evaporation of the water, especially in extremely hot weather. Conditions in the greenhouse made it necessary to add sterile water to the cultures from time to time, usually after each sixth week. Although this was done with all possible precautions contamination, which often destroyed as many as 10 per cent of the experiments, could not be avoided. Therefore all experiments were carried out in triplicate.

It might be mentioned here that a number of different nutrient solutions was tried out with regard to the effect on germination of orchid seeds. The nutrient solutions used were those employed by Artari, Molisch, von der Crone, Nobbe, Pfeffer, Sachs, and three different variations of Knop's solution. Although a definite decision cannot be made at present, the best growth and development were recorded in the nutrient solutions employed by Knop and Sachs. However, the growth of seedlings in these solutions was only 50 per cent of that obtained during the same period in the solutions of Burgeff, Pfeffer, and Knudson's solution "D." Since the nutrient solution "B" employed by Knudson ('22) and the one developed by the writer, here called solution "L," proved most satisfactory, they alone are considered in this paper.

Solution B	
$Ca(NO_3)_2$	1.00 gm.
K_2HPO_4	0.25 gm.
$MgSO_4 . 7H_2O$	0.25 gm.
$Fe_3(PO_4)_2 . 4H_2O$	0.25 gm.
$(NH_4)_2 . SO_4$	0.50 gm.
Sugar	20.00 gm.
Distilled water	1000 cc.

Solution L	
$CaCl_2$	1.00 gm.
KH_2PO_4	1.00 gm.
$MgSO_4 . 7H_2O$	1.00 gm.
$Fe_3(PO_4)_2 . 8H_2O$	0.33 gm.
$(NH_4)_2 . CO_3 . H_2O$	0.50 gm.
$NH_4 . NO_3$	0.50 gm.
Sugar	20.00 gm.
Distilled water	1000 cc.

In general 1.75 per cent agar was added. Preliminary experiments had shown that orchid seeds planted on medium L finally grew as well as in Burgeff's solution. Acid was added in a quantity necessary to bring the pH concentration to the point desired. Of course, in solutions with pH values below 4.8 the percentage of the agar had to be raised in order to render the medium solid enough for the purpose designated. After planting, the culture flasks were placed in the greenhouse at a temperature between 20° and 30° C. and kept covered with cheese-cloth.

It was possible to make measurements with an ocular micrometer attached to the microscope, but only of those seedlings growing close to the wall of the flask. However, since the number of seedlings in one flask never exceeded 300, the seedlings in the same stage of growth and of the same size could be examined with relative ease and the percentage of the different sizes determined.

The seeds used in these experiments were those from *Cattleya* hybrids grown at the Missouri Botanical Garden, and were over one year old. The parents are as follows:

No. 18. *Cattleya Trianae* × *Laelio-Cattleya luminosa aurea.*
No. 21. *Cattleya Trianae* × *Cattleya "Princess Royal" alba.*
No. 27. *Cattleya Trianae (light)* × *Cattleya O'Brieniana.*

In general, the terms used in describing the stages of development are those employed by Knudson ('22); the expression "advanced spherule stage" used in this paper means the period of production of leaves before the formation of the first root.

Experiments

Experiments were carried on with solution B and the writer's solution L, to which had been added levulose, glucose, sucrose, or maltose, as the source of sugar. The seeds were planted on July 19, 1927, and the results here reported recorded on December 29, 1927.

The measurements were taken in the manner described above; for this reason the figures given are only approximate, but are under- rather than over-estimated. The numbers given in the column "succession in superiority" express the following three stages, the average measurements of the embryos being used: (1) average diameter above 1000 μ, (2) average diameter from 500 μ to 1000 μ, and (3) average diameter below 500 μ.

The results of these experiments, recorded in table I, prove that the best growth was obtained in nutrient solutions with maltose as the sugar supply.

TABLE I

CATTLEYA SEEDS PLANTED ON JULY 19, 1927; GROWTH RECORDED ON DECEMBER 29, 1927

No. of seed	Nutrient solution	Diameter of embryo in microns			State of growth	Succession in superiority
		Min.	Max.	Aver.		
18 21 27	Plain B	90 85 100	140 180 200	115 123 150	Small spherule stage; very light green; seedlings apparently dying.	3* 3 3
18 21 27	Solution B + 2% levulose	460 490 500	1200 1500 1400	830 995 950	Seedlings forming leaves; green; healthy.	2 2 2
18 21 27	Solution B + 2% glucose	460 480 450	1100 1200 1300	785 840 875	Seedlings green; forming leaves; well developed.	2 2 2
18 21 27	Solution B + 2% sucrose	450 460 500	1000 900 1100	725 680 800	Seedlings well developed; green; forming leaves.	2 2 2
18 21 27	Solution B + 2% maltose	850 960 1000	1000 1100 1200	925 1030 1100	Seedlings very well developed; green; slender; healthy; forming leaves.	2 1 1
18 21 27	Plain L	100 90 100	180 200 300	140 145 200	Small spherule stage; very light green; leaf point marked.	3 3 3
18 21 27	Solution L + 2% levulose	520 680 700	1350 1400 1500	935 1040 1100	Seedlings well developed; green; healthy; forming leaves.	2 1 1
18 21 27	Solution L + 2% glucose	550 670 540	1150 1350 1450	850 1010 995	Seedings well developed; green; forming leaves.	2 1 2
18 21 27	Solution L + 2% sucrose	490 630 480	1200 1400 1500	845 1015 990	Seedlings well developed; green; forming leaves.	2 1 2
18 21 27	Solution L + 2% maltose	890 860 1000	1400 1500 2000	1145 1180 1500	Seedlings very well developed; dark green; very well developed protocorms; all forming leaves.	1 1 1

* The numbers in this column denote the following stages: 1, average diameter above 1000 microns; 2, average diameter from 500 to 1000 microns; and 3, average diameter below 500 microns.

SOLUTION B

Maltose.—The best growth was recorded in solutions which had been supplied with maltose. Ninety per cent of the embryos were far advanced in growth, having protocorms from 1 to 1.2 mm. in diameter; each had developed two leaves (3 to 6 mm. in length). Ten per cent of the seedlings had already produced one leaf (2 to 4 mm. in length), and a second one half as long as the first was forming. All seedlings had a great number of fine root hairs and appeared healthy. The internodes and petioles were elongated and showed only a very pale green color, this condition resembling the etiolation usually ascribed to lack of nitrogen. However, development of the seedlings was otherwise apparently normal, and the leaves were vigorous, as shown by their large size. The etiolated cases in which growth was retarded may be considered as individual variations (seedlings which because of some internal factors grew more slowly). The pH concentration in these cultures was between 5.2 and 5.4, certainly sufficient to secure normal growth, as preliminary experiments had shown. Seedlings grown on media with a pH concentration above 5.6 showed very slow growth and chlorosis. They were, at the time when the experiments were recorded, in the advanced spherule stage, but were only very light yellowish with a light green spot marking the place of the leaf point. In nutrient solutions with a pH concentration above 6.0 the growth was as poor as in the plain solution without any sugar supply.

Sucrose.—All seedlings were in the advanced spherule stage, about 60 per cent of them having already formed the first leaf (0.5 to 0.8 mm. in length) and the second one just started. The rest of the seedlings were forming the first leaf. All were healthy, but the color of the leaves was not as dark as in those seedlings grown on the maltose medium. The pH concentration of these solutions with sucrose was 5.2. (On the more alkaline media the growth and development of the embryos rapidly decreased, so that at a concentration of 5.6 the seedlings showed severe chlorosis). All were in the advanced spherule stage, but only 9 per cent had formed one leaf measuring 0.3 to 0.5 mm. in length, and the remaining 91 per cent had just reached the advanced spherule stage with the leaf point barely marked. All the embryos were

very light green, except those grown at 5.2, which were almost white, only the leaf point, or in the advanced stage of growth, the leaves, showing a very light green color. Two to three weeks after these experiments were recorded even this very light green color had almost faded away, and the seedlings were apparently dying, being unable to produce chlorophyll and to carry on assimilation.

Glucose.—The development of seedlings on this medium was fairly good. They had well-developed light green protocorms; 22 per cent had already produced two leaves (1 to 1.5 mm. in length); 78 per cent were just forming the first two leaves (0.5 to 1.2 mm. in length), the second leaf one-half the length of the first. All leaves were light green, and all seedlings which had attained full growth of both leaves had formed root-hairs. The pH concentration of the nutrient medium was 5.0. In experiments with higher pH values, likewise in the experiments with maltose and sucrose, a decrease in growth and life processes has been observed. At a pH concentration above 5.6 the development was noticeably retarded; the first indication of chlorosis appeared; the embryos reached the spherule stage and even pointed the first leaf, but were not able to continue in growth. In pH concentrations of about 5.8 and higher the seedlings swelled, but the embryos remained small and showed only very light yellowish green color.

Levulose.—The development of the seedlings on this medium was very satisfactory. The seedlings were dark green, the protocorms very well developed; about 10 per cent had already formed two dark green leaves (2 to 3 mm. in length); 65 per cent had well-developed protocorms and two dark green leaves, the second one-half the length of the first. Twenty-five per cent had not progressed as far in growth and were just forming the first leaf. The effect of the pH concentration was observed to be the same as in the media mentioned above. Of the remaining 25 per cent almost all were forming two dark leaves, the protocorms being green and well developed. Only very few had not progressed as far in growth and were just forming the first leaf.

In one of the cultures made from seed No. 27 about 38 per cent of the seedlings had died in the very first spherule stage; they had

swelled but turned brown before the leaf had been pointed; 7 per cent had passed the advanced spherule stage, had green protocorms and two dark leaves (2 to 3 mm. in length), and appeared very healthy. The failure of those 38 per cent to germinate could be explained only by the weak constitution of the seed, the nutrient medium having been the same as in the other nutrient solutions. This is mentioned merely to make a complete report on the experiments.

Plain nutrient medium.—On this medium without any sugar supply the embryos grew to the small spherule stage, the protocorms being about 90 to 150 μ in diameter and showing a whitish green color with a very light green spot, the leaf point. Apparently they were dying.

SOLUTION L

Maltose.—As in solution B, in solution L, the best growth of the seedlings was registered with maltose. The embryos were very well developed, with large and dark green protocorms (1 to 2 mm. in length) and dark green leaves. Eighty per cent of the seedlings had already formed the first leaf (2 to 3 mm. in length), the second one being half the length of the first. Ten per cent had passed through the small spherule stage and the first leaf was forming. Ten per cent had two leaves (2 to 5 mm. in length) and were forming the third one. The seedlings on this nutrient medium had the largest protocorms of any in these experiments; the protocorms were green, the leaves dark green, and the seedlings with developed leaves had formed root-hairs. All seedlings appeared normal, there being no unusual elongation of the internodes or the petioles, even though they were very crowded. It seems to be necessary to mention this fact, because one might suspect that in solution B with maltose the crowded condition of the seedlings might have caused the kind of etiolation mentioned above. The seedlings were in the best state of growth and health. The pH concentration of this nutrient medium was about 5.2. Another fact which ought to be brought out is that some of the seedlings with developed leaves showed the first signs of root formation.

Sucrose.—The seedlings on this medium were well developed with green protocorms and leaves somewhat darker, but not as

dark as in the cultures with maltose. Eighty per cent of the embryos had already formed one leaf (0.5 to 1 mm. in length) and were forming the second one about one-third the length of the fully developed leaf. Fifteen per cent were forming the first leaf (half of the full length), and 5 per cent were in the advanced spherule stage, just forming the first leaf. All seedlings appeared healthy, and those with developed leaves had formed root-hairs. The pH concentration was about 5.2.

Glucose.—The seedlings grown on glucose medium were fairly well developed and green with a well-developed protocorm. Sixty-eight per cent had two leaves (1 to 1.5 mm. in length); 32 per cent were forming the first leaf which was about 0.3 to 0.8 mm. in length. The embryos with developed leaves were forming root-hairs. The seedlings on glucose medium developed somewhat differently from those grown on a maltose or levulose medium. They grew more slowly and were light green, the leaves or the leaf points being dark green. The pH concentration was 5.2. On media with a pH value of 5.6 and above, decided chlorosis was noticed, and at a pH value of about 6.0 the growth equalled that on plain nutrient medium without any sugar supply.

Levulose.—Twelve per cent of the seedlings were dark green. The protocorms were very well developed, and compared to those on the other media were second largest in diameter. They had two developed leaves (1.5 to 2 mm. in length) and were forming root-hairs. Seventy per cent of the seedlings were dark green with one developed leaf (1 to 1.5 mm.), and 18 per cent were in the advanced spherule stage, just beginning to form the first leaf. Although the protocorms and leaves were well developed the growth was apparently slower than on the other media at the same pH concentration. The most favorable hydrogen-ion concentration was about 5.2.

Plain nutrient medium.—On this medium without any sugar supply the seedlings had reached the small spherule stage, the protocorms measuring about 90 to 200 μ in diameter. They had attained the same stage of growth in 5 months as those grown on sugar media in 4 to 6 weeks. The protocorms were very light green and showed a darker spot, the leaf point, and some of the seedlings had started to form a leaf (20 to 50 μ in length). Ap-

parently, however, they were not capable of carrying on assimilation. One month after these records were taken (January 29, 1928) the seedlings were still alive.

Discussion

Summarizing these results in a synoptical table we have the following data regarding the development on the different media.

TABLE II

	Solution B	Solution L
Plain	Very weak growth; seedlings apparently dying.	Weak growth; leaf-point weakly marked; continuation of growth doubtful.
+ levulose	10% with two developed leaves; 65% with one developed leaf, forming the second one; root hairs; 25% forming the first leaf. All apparently healthy.	12% with two developed leaves and root-hairs; 70% with one developed leaf; 18% in the advanced spherule stage, forming the first leaf.
+ glucose	22% with two developed leaves and root-hairs; 78% with one leaf, forming the second. Healthy.	68% with two developed leaves and root-hairs; 32% forming the first leaf. Healthy.
+ sucrose	60% with one developed leaf, the second forming; 40% forming the first leaf.	80% with one developed leaf, the second forming; root-hairs; 15% forming the first leaf; 5% in the advanced spherule stage.
+ maltose	90% with two fully developed leaves and root-hairs; 10% with one fully developed leaf, and one half-developed; root-hairs. Healthy.	10% with two fully developed leaves, forming the third, also roots; 80% with one fully developed and one half-developed leaf and root-hairs; 10% forming first leaf.

The practically negative results obtained on plain nutrient media without any sugar supply are in agreement with those of other investigators who dealt with the same subject. Although the seedlings in these solutions were still living when the data were taken, there is no doubt that they would gradually have died. This fact was proved also in a number of preliminary experiments performed in this laboratory. The conclusion that orchid seedlings grown under aseptic conditions on sugar-free media are not capable of germination is therefore highly plausible. It might be emphasized that a slight difference in the development in solution L from that in solution B was noticed, as is indicated in

the tables. While in solution B the embryos had reached only the small spherule stage and the leaf point was not even marked, those in solution L had passed through this stage and had a leaf point, although very weakly marked; some few of them had even tried to form a leaf, but apparently were unable to continue growing.

The best growth occurred on media supplied with maltose, especially in solution L. The seedlings grown on medium B were very well developed and healthy in appearance, but the protocorms were slender, the leaves narrow and lying at full length. The diameters of the protocorms in solution B were as much as 36 per cent shorter than of those grown in solution L. Referring to Knudson's experiments on symbiosis with different fungi on media supplied with starch, it is very probable that the favorable effect of certain fungi upon germination and development of orchid seeds might be ascribed to the fact that those fungi in question, by enzymatic processes, transform the starch to sugars, which are better digested by the orchid embryos, and that their metabolic processes render the medium more acid, thus favoring enzyme action. A similar explanation could be assumed in cases where a favorable effect of bacteria and yeasts had been reported. Knudson says: "When starch is provided as the organic matter in the culture media, there is no germination unless the fungus is supplied." The facts that no germination took place on starch-media not inoculated with a fungus, as reported by Knudson, and that the starch remained untouched, show distinctly that orchid seeds do not possess enzymes to transform the starch to sugar, and that they therefore are unable to use this food supply. Burgeff ('09) reports that the best growth of the symbiotic fungi was recorded on media containing agar, rain-water, and a small supply of starch. He also points out that for those fungi maltose was a better source of sugar than saccharose. From the fact that in starch hydrolysis maltose is the final product which can be transformed to glucose, also from the results obtained in the experiments reported in this paper, and finally, from the evidence that glucose is not an especially favorable sugar supply for orchid embryos, we may conclude that maltose is probably one of the best-suited foods for orchid seedlings. The probability is that

the hydrolysis of maltose to glucose furnishes energy to the growing plant. Additional credence is given this supposition by Bernard's ('09) report in which he states that the starch is transformed to sugar when the symbiotic fungus enters the cells of the germinating orchid seeds.

There is no doubt that the orchid seed contains a supply of sugar, although in very small amounts. In many tests made on seeds of Cattleya, Laelio-Cattleya, Brasso-Cattleya, etc., the author has always found reducing sugars. Burgeff (*l. c.*, p. 70–71) mentions that a yellow coloring matter goes into solution if orchid seeds are allowed to stand for several days in water; he supposes that this undetermined matter, which reduces Fehling's solution and therefore has the qualities of a sugar, attracts the symbiotic fungus. This undetermined reducing sugar might be considered the only source of carbohydrate for the germinating seed. If it is used up and no other suitable carbohydrate is available the embryo is doomed to die.

If we suppose the protocorms to be spheres and calculate the volume of those spheres from the average-measurements given in table I, we will find a difference in volume of as much as 2.5 times. However, the smaller the volume the less is the assimilation. This difference in the ratio of assimilation indisputably has an influence upon the growth and development of the seedlings. It is a question whether the constitution of solution L causes this difference in development. Certainly the vigorous growth of the protocorms indicates a healthy development, since the nutrient material obtained from the nutrient solution is evidently not only sufficient to maintain growth, but there is undoubtedly a surplus of material which is stored in the tissue of the protocorm.

Also the pH concentration of the medium is of great importance, a fact which was brought into prominence by Knudson and proved by Clement. As has been mentioned above, in nutrient solutions with pH values of 5.2 and below the growth takes place in a normal fashion; above 5.2 growth is markedly retarded and signs of chlorosis appear. Hydrogen-ion concentrations of about 6.0 and above are very unfavorable for growth. Usually the seeds do not germinate at all, and if they do chlorosis takes place and the seeds die after they have reached the small spherule

stage. The favorable effect of a symbiotic fungus is explained by the additional fact that the fungus produces acid, thus changing the pH concentration of the less favorable medium to one more favorable, a fact also pointed out by Knudson, as mentioned above. This indicates that when the seed is planted under aseptic conditions on a maltose medium, for example, enzymes are present in small quantities and these in turn are stimulated or retarded in their activity by acid or basic conditions.

Since hydrochloric acid was used in order to adjust the pH concentration, the amount of chloride is higher in solution L than in solution B, which contains no chlorides in the original composition. Preliminary experiments have demonstrated that the effect of chlorine on growth is not of importance, and the effect on germination is problematical; likewise it is doubtful whether the treatment of seeds before planting (with chlorinated lime) has a stimulating effect upon germination. Seeds taken under aseptic conditions from a seed pod and planted without sterilization directly on the medium germinated as well as those treated before planting with the sterilizing solution in question. This, however, does not exclude the possibility of stimulating seed germination by *hypotonic* chloride solutions when Popoff's ('25) method is employed.

A comparative examination of the two nutrient solutions shows that there is, theoretically, 5 times more potassium in solution L; further 4 times as much phosphate, and about 16 per cent more nitrogen. At first it would seem to be impossible to apply a nutrient solution of such composition, but we must take into account the fact that a relatively large amount of salt is precipitated when the solution is subjected to sterilization and to titration with either acids or alkalies. That precipitate consists, as far as could be determined qualitatively in default of an equipment for quantitative analyses, of C, K, P, and Fe, and we may suppose that the difference is not as striking as it appeared from the first. We assume that the amount of nitrogen was increased slightly, the amount of both potassium and phosphorus, many times. What is the effect upon germination and growth? According to the records summarized in the tables the development in solution L was, in general, 5 to 10 per cent better than in solution B. The

seedlings appeared darker in color and had progressed relatively further in development. This effect might be ascribed to the larger dose of phosphorus and potassium. Maiwald ('23) and Schertz ('29) found, in experiments on potato and cotton plants, a correlation between phosphorus, potassium, and nitrogen and the formation of chloroplast pigments. Nitrogen increased the amount of pigments, large amounts of phosphorus produced more chloroplasts than potassium and less than nitrogen, large amounts of potassium evidently suppressed pigment formation. Stoklasa ('16) has proved that the potassium ion plays an important part in the processes of metabolism. Clements' ('28) studies on the nutrition of pea seeds indicate that KH_2PO_4 has a very marked influence on nitrogen assimilation, and also that a satisfactory balance between nitrogen and carbohydrates is of importance. The results of the experiments in solution L can be interpreted as the effect of large doses of potassium on the synthesis of proteins (Weever, '11) and the assimilation of nitrogen, an effect connected with an increase in assimilation of carbohydrates. It must be borne in mind, however, that assimilation is also dependent on the nature of the sugars and the presence of proper enzymes in the organism. The activity of enzymes, in turn, appears to be dependent to some extent on the pH concentration of the medium.

Summary

1. Of the sugars used in these experiments maltose was found to be most favorable for the germination and growth of *Cattleya* seeds. According to their effect upon growth, the other sugars rank as follows: levulose, glucose, and saccharose.

2. The hydrogen-ion concentration is of great importance in germination and development of *Cattleya* seeds, much better growth occurring in solutions with a pH value between 4.8 and 5.2.

3. On media with a pH value at or above 5.6 germination and growth are retarded and in most instances chlorosis takes place. With a pH value of 6.0 and higher there is extreme chlorosis and the seedlings are unable to germinate.

4. On glucose and sucrose, the least favorable carbohydrate sources, the seedlings develop more slowly and chlorophyll is formed less rapidly, even at the most favorable pH concentration.

5. A nutrient solution, solidified with agar, of a composition different from Knudson's solution B was tried. The growth and development on this medium are better than on solution B.

6. Factors involved in this problem are discussed.

Acknowledgements

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Literature Cited

Bernard, N. ('09). L'evolution dans la symbiose. Les orchidées et leurs champignons commensaux. Ann. Sci. Nat. Bot. IX. **9**: 1–191. 1909.

Burgeff, H. ('09). Die Wurzelpilze der Orchideen, ihre Kultur und ihr Leben in der Pflanze. Jena, 1909.

Clement, E. ('24). Germination of Odontoglossum and other seeds without fungus aid. Orchid Review **32**: 233–238. 1924.

————, ('26). The non-symbiotic germination of orchid seeds. *Ibid.* **34**: 164–169. 1926.

————, ('29). Non-symbiotic and symbiotic germination of orchid seeds. *Ibid.* **37**: 68–75. 1929.

Clements, H. F. ('28). Plant nutrition studies in relation to the triangular system of water cultures. Plant. Physiol. **3**: 441–458. 1928.

Constantin, J., et Magrou, J. ('22). Actualités Biol. Applications industrielles d'une grande découverte francaise. Ann. Sci. Nat. Bot. X. **4**: i–xxxiv. 1922.

Knudson, L. ('22). Nonsymbiotic germination of orchid seeds. Bot. Gaz. **73**: 1–25. 1922.

————, ('24). Further observations on nonsymbiotic germination of orchid seeds. *Ibid.* **77**: 212–219. 1924.

————, ('25). Physiological study of the symbiotic germination of orchid seeds. *Ibid.* **79**: 345–379. 1925.

————, ('27). Symbiosis and asymbiosis relative to orchids. New Phytologist **26**: 328–336. 1927.

Maiwald, K. ('23). Wirkung hoher Nährstoffgaben auf den Assimilations-apparat. Angew. Bot. **5**: 33–48, 49–74. 1923.

Popoff, M. ('23). Über Zellstimulantien und ihre theoretische Begründung. Jahrb. Univ. Sofia. 1923.

————, ('25). Zellstimulantien und ihre theoretische Begründung. Zellstimulationsforschungen **1**: 3–38. 1925.

Ramsbottom, J. ('22). The germination of orchid seeds. Orchid Review **30**: 197–202. 1922.

Schertz, F. M. ('29). The effect of potassium, nitrogen and phosphorus fertilizing

upon the chloroplast pigments, upon the mineral content of the leaves, and upon production in crop plants. Plant Physiol. **4**: 269–279. 1929.

Stoklasa, J. ('16). Ist das Kaliumion an der Eiweisssynthese in der Pflanzenzelle beteiligt? Biochem. Zeitschr. **73**: 107–160. 1916.

Weever, Th. ('11). Untersuchungen über die Lokalisation und Funktion des Kaliums in den Pflanzen. Rec. Trav. Bot. Neerlandais **8**: 289–332. 1911.

Wilson, J. K. ('15). Calcium hypochloride as a seed sterilizer. Am. Jour. Bot. **2**: 420–427. 1915.

Explanation of Plate

PLATE 42

Fig. 1. Cattleya seedlings No. 27 grown on medium L + 2 per cent maltose. × 9/16.

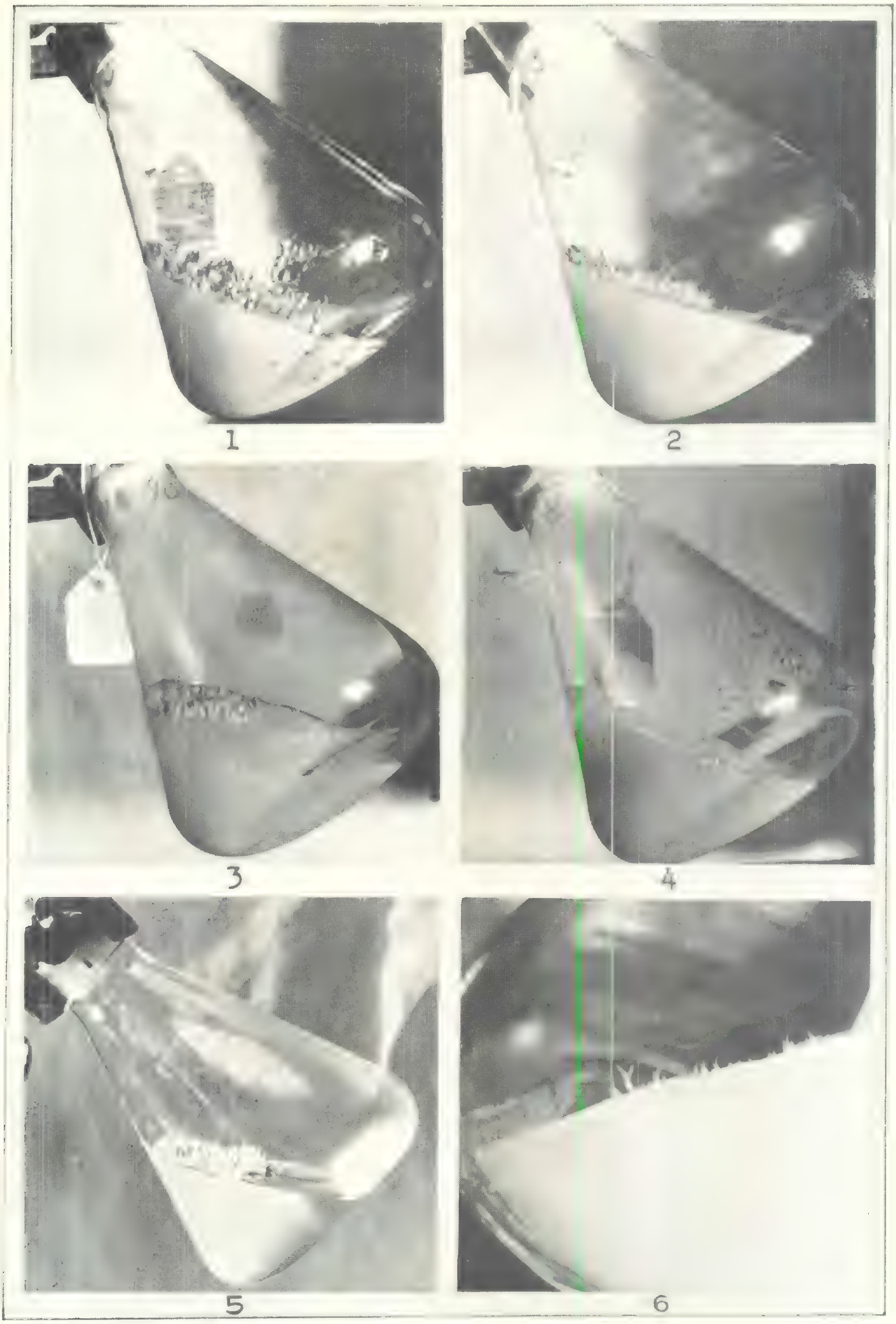
Fig. 2. Cattleya seedlings No. 27 grown on medium B + 2 per cent maltose. × 9/16.

Fig. 3. Cattleya seedlings No. 21 grown on medium L + 2 per cent sucrose. × 9/16.

Fig. 4. Cattleya seedlings No. 21 grown on medium B + 2 per cent sucrose. × 9/16.

Fig. 5. Cattleya seedlings No. 27 grown on medium L + 2 per cent maltose, showing chlorosis as consequence of a pH concentration of about 5.8. × 1/2.

Fig. 6. Cattleya seedlings No. 27 grown on medium L + 2 per cent sucrose; the first two seedlings on the left side are shown growing on the top of other seedlings. Natural size.



LA GARDE—ORCHID GERMINATION

GENERAL INDEX TO VOLUME XVI

New scientific names of plants and the final members of new combinations are printed in **bold face** type; synonyms, and page numbers having reference to figures and plates, in *italics;* and previously published names and all other matter, in ordinary type.

A

Abutilon, species of, *216:* effect of infectious chlorosis on, 130, 158, 159, *220;* effect of continuous light on, 177, *214*, *218*, of short-day illumination on, 178, *222*, of total darkness on, 180; effect of removing variegated leaves, *226;* grafting experiments with, 187, *218;* histological studies of, subjected to various conditions of light, 182; transmission of infectious chlorosis in, by means of inoculations, 184

Acanthostigmella genuflexa, 288, *358;* **Thaxteri,** 321, *376*

Acidity in variegated leaves, 171, 189; electrometric determinations of, 189, 196; effect of exposure to air on, 193

Agave **scaphoidea,** 391; utahensis, 389, var. **nevadensis,** 390, *392*

Agaves, New, from southwestern United States, 389

Amsonia, A new species of, from the south-central states, 407

Amsonia **illustris,** 407; ludoviciana, 409; salicifolia, 410; Tabernaemontana var. Gattingeri, 407, var. salicifolia, 410

Anderson, Edgar. Variation in Aster anomalus, 129

Apocynaceae, Studies in the, IIIA, 407

Ascospores of Daldinia, experiments in germination of, 417

Aster anomalus, 130, *144*, Variation in, 129; azureus, 131, *144;* oblongifolius, 131; Shortii, 131, 137; turbinellus, 137, *144*

Auricularia, 49

B

Byssosphaeria helicophila, 320

C

Calcium in variegated leaves, 170

Calcium chloride solutions, tolerance map for collards in, *63;* average root-hair elongation in, *67*, maximum, *67*

Calcium hydroxide, average root-hair elongation in, *67*, maximum, *67*

Calcium nitrate: average root-hair elongation in, 55, *56*, *67;* maximum root-hair elongation in, 57, *67;* pH-molar rate relation for collards in, 53; root and root-hair elongation in .004 *M*, 55, *61*, in .012 *M*, *61*, 62, in .020 *M*, 62, *62*

Carbon dioxide: assimilation products of, in variegated leaves, 170; relation of, to infectious chlorosis, 158

Cattleya Trianae: X Laelio-Cattleya luminosa aurea, 502, X Cattleya "Princess Royal" alba, 502, X Cattleya O'Brieniana, 502

Cercospora, 1; A host index to the North American species of the genus, 1, 9; host families of, 51; index to species of, 29

Cercospora, 3; Apii, 3; Chenopodii, 3; ferruginea, 3; penicillata, 3

Cercosporella, 4; cana, 4; persica, 4

Chaetosphaeria parvicapsa, 322

Child, Marion. Preliminary studies in the genus Daldinia, 411

Chlorine, effect of, on growth of orchid seedlings, 511

Chlorosis, infectious: host range of, 162; in variegated plants, Some chemical and physiological studies on the nature and transmission of, 145; theories concerning, 165

Clathrosphaeria, 331

Climatic factors, relation of, to infectious chlorosis, 158

Clinoconidium, 342; *farinosum*, 343

Collards, The pH-molar rate relation for, in calcium nitrate, 53

Cystobasidium, 491

D

Daldinia, Preliminary studies in the genus, 411

Daldinia, 411; cingulata, 412; concentrica, 412, germination of ascospores of, 417, *484*, *486*, morphology of, 475, mycelial growth of, 456, *482;* Escholzii, 415; loculata, 412; vernicosa, 412, germination of ascospores of, 418, *484*, *486*, morphology of, 475, mycelial growth of, 456, *482;* X, 412, germination of ascocpores of, 418, *486*, morphology of, 475, mycelial growth of, 456, *482;* Y, 412, germination of ascospores of, 418, morphology of, 475, mycelial growth of, 456, *482*

Darkness, effect of, on variegated plants, 180
Davis, E. F. Some chemical and physiological studies on the nature and transmission of infectious chlorosis in variegated plants, 145
Delortia, 338; *lignitalis*, 336; palmicola, 338, *384*
Dodge, Carroll W., Zeller, S. M. and. Hysterangium in North America, 83
Drepanoconis, 341; **anguisporus,** 344, *384*; *brasiliense*, 343; *fructigena*, 343; larvaeformis, 343, *384*

E

Electrometric determinations of hydrogen-ion concentration, 189, 196, apparatus used in, *224*
Enzymes, effect of, on germination of ascospores, 425
Eryngium mexicanum, 395; *mexicanum*, 395; phyteumae, 395; **Wolffii,** 395
Everhartia, 335; **candida,** 337, *384*; hymenuloides, 337, *384*; lignitalis, 336, *384*
Evonymus, effect of continuous illumination on, 176; effect of short-day illumination on, 179; effect of total darkness on, 180; grafting and budding experiments with, 186; transmission of infectious chlorosis in, by means of inoculations, 185; variegated leaves of, *216*, *220*, *226*

F

Farr, Clifford H. Studies in the growth of root hairs in solutions, IX, 53
Freezing: effect of, on acidity of juice from variegated leaves, 193; effect of, on buffer action, 199; and ultra-violet radiation, effect of, on germination of ascospores of Daldinia, 428
Fungi Imperfecti, A monograph of the Helicosporous, 227

G

Gaura suffulta Engelmann, 399
Germination of ascospores of Daldinia, 417: effect of different media on, 440; effect of enzymes on, 425; effect of hydrogen-ion concentrations on, 450; effect of temperature on, 431; effect of ultra-violet radiation on, 427; experiments with old ascospores, 417, with fresh ascospores, 422
Germination of orchids, non-symbiotic, 499
Glucose, growth of Cattleya seedlings on media containing, 505, 507
Grafting: transmission of infectious chlorosis by, 150; and budding experiments with variegated and green plants, 186
Greenman, J. M. A new variety of Senecio aureus L., 405; and Eva M. Fling Roush. New agaves from southwestern United States, 389
Gyroceras nymphaearum, 294; plantaginis, *388*

H

Helicodendron, 329; **fuscum,** 332, *380*; **hyalinum,** 333, *380*; paradoxum, 329; **triglitziensis,** 330, *380*, *386*; **tubulosum,** 330, *380*
Helicodesmus, 329; *albus*, 330
Helicoma, 295; ambiens, 310, *368*, *372*; *ambiguum*, 273; **asperothecum,** 311, *372*; **atroseptatum,** 307, *372*; *bambusae*, 319; *Berkeleyi*, 304, 318; *binale*, 318, var. *apertum*, 318; **candidum,** 316, *374*; **conicodentatum,** 311, *374*; Curtisii, 312, *368*, *386*, *388*; fasciculatum, 315, *374*; *griseum*, 285; **intermedium,** 306; *larvale*, 322; limpidum, 301; **microscopicum,** 299, *364*; **minutissimum,** 298, *364*; monilipes, 302, *364*; **Morgani,** 304, *366*; Mülleri, 307, *368*; **olivaceum,** 302, *364*; **palmigenum,** 306; **perelegans,** 303, *366*; phaeosporium, 304, *370*; polysporum, 300, *364*; **proliferens,** 309, *370*, *388*; **recurvum,** 312, *374*; repens, 300; **roseolum,** 297, *364*; **simplex,** 315, *374*; **stigmateum,** 298, *364*; velutinum, 305, *370*; **violaceum,** 303, *366*
Helicoma, 317
Helicomyces, 270; *albus*, 271, 275; **ambiguus,** 273, *350*; *anguisporus*, 344; *aureus*, 279; bellus, 273; *brunneolus*, 308; *candidus*, 316; *cinereus*, 282; *clarus*, 271; *Curtisii*, 313; *diplosporus*, 319; *elegans*, 271; *fasciculatus*, 315; *fuscus*, 288; *gracilis*, 281; *larvaeformis*, 343; *microscopicus*, 299; mirabilis, 340; *Mülleri*, 308; *niveus*, 298; *olivaceus*, 277; roseus, 271, *350*; scandens, 274, *350*, *386*, *388*; *sphaeropsidis*, 298; tenuis, 272; *triglitziensis*, 330; *tubulosus*, 330; *vegetus*, 277
Helicoon, 322; auratum, 325, *378*; ellipticum, 326, *378*, *388*; *Fairmani*, 325; **farinosum,** 324, *378*; **fuscosporum,** 326, *378*; politulum, 328; **reticulatum,** 327, *378*; **Richonis,** 323; sessile, 325, *378*; *thysanophorum*, 332; *tubulosum*, 331
Helicopsis, 295; *olivaceus*, 302; *punctata*, 302

Helicoryne, 295; *ramosa*, 327; *viride*, 307
Helicosporium, 275; albidum, 287; albo-carneum, 290; *ambiens*, 310; *auratum*, 325; **aureum,** 279, *354*, *386*; *Berkeleyi*, 318; *binale*, 319; *Boydii*, 305; *brunneolum*, 308; brunneum, 291; *cinereum*, 282; *Curtisii*, 312; **decumbens,** 284, *356*; *diplosporum*, 319; **Elinorae,** 290, *362*; *ellipticum*, 327; Ellisii, 291; *fasciculatum*, 315; *Fuckelii*, 277; *fuscum*, 332; **gracile,** 281, *352*, *354*; griseum, 285; *griseum*, 282, *356*; **guianensis,** 280, *352*; herbarum, 292; *intermedium*, 306, var. *palmigenum*, 306; *leptosporum*, 282; *limpidum*, 301; lumbricoides, 282, *356*, *388*; *lumbricoides*, 282; **lumbricopsis,** 284, *358*, *360*; *microscopicum*, 299; *monilipes*, 302; *Mülleri*, 307; **nematosporum,** 288, *362*; *nymphaearum*, 294; *olivaceum*, 277; pallidum, 286, *358*; *phaeosporium*, 304; phragmites, 287, *358*; *pilosum*, 279; *politulum*, 328; *polysporum*, 300; populi, 293; prasinum, 293; pulvinatum, 293; *pulvinatum* var. *effusum*, 277; *ramosum*, 327; *recurvum*, 312; *repens*, 300; *Richonis*, 323; **serpentinum,** 288, *360*; *simplex*, 315; *spectabile*, 304; *thysanophorum*, 332; *Tiliae*, 313; vegetum, 277, *352*; *velutinum*, 305; *viride*, 308
Helicostilbe, 333; *helicina*, 274, **simplex,** 334, *382*
Helicostilbe, 333
Helicotrichum, 276; *albo-carneum*, 290; *brunneum*, 291; *candidum*, 316; *populi*, 293; *pulvinatum*, 277, 293
Herpotrichia pezizula, 314
Hobsonia, 339; *Ackermanni*, 340; gigaspora, 340, *382*; **mirabilis,** 340, *382*, *388*
Host index to the North American species of the genus Cercospora, 1
Host relations in infectious chlorosis, 158
Houstonia Croftiae Britton & Rusby, 401, *404*; humifusa, 401, *404*; parviflora, 402, *404*
Hydrogen-ion concentration: effect of different, on ascospore germination in Daldinia, 450; effect of, on radial growth of mycelium, 471; molar rate relation for collards in calcium nitrate, 53; of leaf juices from variegated leaves, 189; of medium, effect of, on growth of Cattleya seedlings, 510
Hyperrhiza, 83
Hysterangium in North America, 83
Hysterangium, 83; affine, 92, *126*, *128*, var. irregulare, 93, var. tenuispora, 93; **album,** 87, *124*, *128*; australe, 102; *australe*, 102; calcareum, 119, *128*; cinereum, 103; **cistophilum,** 107, *126*, *128*; clathroides, 93, *126*, *128*, var. crassum, 96; *clathroides*, 96, 107, 112, var. *cistophilum*, 107, var. *mutabile*, 112; coriaceum, 113; crassirhachis, 101, *124* *128*; *Eucalyptorum*, 93; **Fischeri,** 109, *124*, *128*; fragile, 118; fuscum, 105, *128*; fusisporum, 121; *Gardneri*, 105; **Harknessii,** 102, *128*; inflatum, 98, *126*, *128*; *Marchii*, 121; membranaceum, 104, *128*; neglectum, 88, *128*; neocaledonicum, 113, *128*; nephriticum, 99, *128*; *niger*, 122; obtusum, 97, *128*; occidentale, 89, *128*; Petri, 119; Phillipsii, 91, *128*; Pompholyx, 106, *128*; *Pseudo-Acaciae*, 122; pumilum, 115, *124*, *128*; **purpureum,** 110, *124*, *128*; Rickeni, 117; *rubescens*, 112; rubricatum, 105, *128*; siculum, 114; Nr. 258, 109; stoloniferum, 111, *128*, var. **rubescens,** 112; *stoloniferum* var. *americanum*, 94; **strobilus,** 90, *124*, *128*; **Thaxteri,** 114, *126*, *128*; Thwaitesii, 116, *128*; viscidum, 120

I

Illumination: continuous, effect of, on infectious chlorosis, 174; short-day, effect of, on infectious chlorosis, 178; total darkness, effect of, on infectious chlorosis, 180
Infectious variegations, physiology and pathology of, 150
Inoculation, transmission of leaf variegation through, 152, 184
Insects, transmission of infectious chlorosis by, 152
Iola, 488

K

Kitaibelia vitifolia, showing infection through grafting, 218
Knudson's Solution B, as a medium for growing orchids, 501, 503

L

Laburnum, infectious chlorosis in, 159
La Garde, Roland V. Non-symbiotic germination of orchids, 499
La Garde's Solution L, as a medium for growing orchids, 501, 506
Lasiosphaeria **Elinorae,** 290, *362*; **nematospora,** 289, *362*; pezizula, 314, *368*
Lavatera arborea, infectious chlorosis in, 159
Leonian agar, effect of: on germination of ascospores of Daldinia, 440; on growth of mycelium of Daldinia, 463, 465, 467, 468

Levulose, growth of Cattleya seedlings on medium containing, 505, 507
Lieneman, Catharine. A host index to the North American species of the genus Cercospora, 1
Life history and cytology of Saccoblastia intermedia, n. sp., 487
Light: effect of intensity of, upon variegation of leaves, 156; effect of quality of, upon variegation of leaves, 157, 172; and darkness, effect of, on growth of mycelium of Daldinia, 456
Ligustrum vulgare, variegation in leaves of, 158
Linder, David H. A monograph of the Helicosporous Fungi Imperfecti, 227; The life history and cytology of Saccoblastia intermedia, n. sp., 487
Lituaria stigmatea, 298

M

Maltose, media containing: effect of, on germination of ascospores of Daldinia, 443; growth of Cattleya seedlings on, 503, 506
Malvaceae, infectious chlorosis in, 156, 159
Marsonia fructigena, 343
Mathias, Mildred E. Notes on southwestern plants, I, 399, II, 401; Studies in the Umbelliferae, II, 393
Media: effect of different, on germination of ascospores of Daldinia, 440; effect of different, on growth of mycelium of Daldinia, 462; for growing orchids, 501; plain nutrient, 506, 507
Melanomma helicophilum, 320
Monograph of the Helicosporous Fungi Imperfecti, 227
Morphological characters of the ascocarp and asexual stage of species of Daldinia, 475
Mycelium of Daldinia: factors influencing the growth of, 456; effect of light and darkness on, 456; effect of different media and different temperatures on, 462; effect of different hydrogen-ion concentrations on, 471
Mylitta Pseudacaciae, 123
Mylittaea Pseudo-Acaciae, 123

N

Neoparrya, A new genus of the Umbelliferae, 393
Neoparrya lithophila, 393, *398*
Nerium Oleander, 409
Nitrogen: effect of, on growth of Cattleya seedlings, 512; in variegated leaves, 171
Nodulisporium Tulasnei, 414
Non-symbiotic germination of orchids, 499
Notes on southwestern plants, I, 399, II, 401
Nutrient relations in variegated leaves, 170
Nutrition of the fungi, 462

O

Oatmeal agar: effect of, on germination of ascospores of Daldinia, 441; effect of, on mycelial growth, 464, 466, 467, 469
Orchids: Non-symbiotic germination of, 499; "advanced spherule stage" of, 502; reducing sugars in seeds of, 510
Osmotic pressure in variegated leaves, 170
Oxygen, effect of, on germination of ascospores of Daldinia, 422

P

Pepsin solutions, effect of, on germination of ascospores of Daldinia, 427
Pfeffer medium: effect of, on germination of ascospores of Daldinia, 441; effect of, on mycelial growth, 464, 465, 467, 469
Phosphorus: effect of, on growth of Cattleya seedlings, 512; in variegated leaves, 170
Pigments in variegated leaves, 169, 188
Pimpinella, A new, to North America, 396
Pimpinella Saxifraga, 396, subsp. nigra, 396
Platanus decoction: effect of, on germination of ascospores of Daldinia, 441; effect of, on mycelial growth, 463, 465, 466, 468
Potassium: effect of, on growth of Cattleya seedlings, 512; in variegated leaves, 170
Prune decoction, effect of, on germination of ascospores of Daldinia, 441

R

Rhizobium sp., 123
Rhizopogon **Marchii,** 121; **niger**, 122; *virens*, 94; *virescens*, 94
Robinia Pseudacacia, 123
Root, general observations upon the, in response to different solutions, 69
Root hairs in solutions, Studies on the growth of, IX, 53
Roush, Eva M. Fling, J. M. Greenman and. New agaves from southwestern United States, 389

S

Saccoblastia caroliniana, 487; **intermedia,** 488; sebacea, 487, var. pruinosa, 487; subardosiaca, 487
Saccoblastia **intermedia,** n. sp., The life history and cytology of, 487
Saccogloea, 487
Senecio aureus L., A new variety of, 405
Senecio aureus, 405, var. **Ashei,** 406, *406;* tomentosus, 405
Septobasidium album, 491
Seseli Nuttallii, 393
Sida Abutilon, variegation in leaves of, 159
Soil and mineral nutrients, relation of, to infectious chlorosis, 158
Sorbus Aucuparia, variegation in leaves of, 159
Southwestern plants, Notes on, I, 399, II, 401
Sphaeria helicoma, 229; *helicophila,* 320; *pezizula,* 314
Splanchnomyces, 83; *clathroides,* 94; *membranaceus,* 104; *nephriticum,* 99
Starch in variegated leaves, 170
Sterilization of orchid seeds, 501
Studies in the Apocynaceae, 407
Studies in the Umbelliferae, II, 393
Sucrose: germination of ascospores of Daldinia on media containing, 419; growth of Cattleya seedlings on media containing, 503, 506
Sugars: effect of medium containing, on germination of ascospores, 443; effect of various, on growth of Cattleya seedlings, 503, 506
Symbiotic fungus, effect of a, on germination of orchid seedlings, 511

T

Temperature: effects of, on germination of ascospores of Daldinia, 431; effect of, on growth of mycelium, 463; in relation to growth on various media, 438
Troposporella, 334; fumosa, 335, *384*
Troposporium, 345; album, 345

U

Ultra-violet radiation, effect of, on germination of ascospores of Daldinia, 427
Umbelliferae, Studies in the, II, 393
Uredinales, 491
Uredo farinosa, 343

V

Variation in Aster anomalus, 129
Variegated plants, Some chemical and physiological studies on the nature and transmission of "infectious chlorosis" in, 145
Variegations, leaf, anatomy of, 166; chemistry of, 169; general physiology and pathology of, 148
"Virus" theory of infectious variegation, 150, 165

W

Woodson, Robert E. Jr. Studies in the Apocynaceae, IIIA, 407

X

Xenosporella, 317; **Berkeleyi,** 318, *376;* **larvalis,** 322, *376;* pleurococca, 318, *376;* **Thaxteri,** 320, *376*

Z

Zeller, S. M. and Carroll W. Dodge. Hysterangium in North America, 83

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